

A Test of Potential Pleistocene Mammal Seed Dispersal in Anachronistic Fruits Using Extant Ecological and Physiological Analogs

Madison J. Boone¹, Charli N. Davis¹, Laura Klasek¹, Jillian F. del Sol¹, Katherine Roehm¹, and Matthew D. Moran^{1,*}

Abstract - Using *Elephas maximus* (Asian Elephant) and *Equus ferus caballus* (Domesticated Horse) as ecological analogs to extinct Pleistocene mammals, we tested the effect of gut passage on 3 proposed anachronistic fruits: *Diospyros virginiana* (American Persimmon), *Maclura pomifera* (Osage Orange), and *Asimina triloba* (Paw Paw). We found that elephant-gut passage of persimmon seeds increased their germination success and decreased their time to sprout, while Osage Orange seeds showed no benefit to gut passage. Neither American Persimmon nor Osage Orange seeds survived gut passage through horses. Both mammals refused to consume Paw Paw fruits. Assuming a similar physiology and behavior compared to our modern analogs, we suggest that extinct North American elephant species could have been important seed dispersers for American Persimmons but were unlikely to be effective for Osage Orange or Paw Paw, while horses would have been poor dispersers for all plant species tested.

Introduction

An anachronistic fruit is defined as one that lacks any apparent seed-dispersing mechanism (Barlow 2001). These fruits tend to be large and fleshy with high nutritional quality, characteristics that make them likely candidates for dispersal by endozoochory, in particular dispersal via ingestion by large vertebrate animals (Janzen 1982). Between 10,000 to 12,000 years ago at the end of the Pleistocene epoch, many lineages of North American mammals went extinct. This extinction event included 35 genera and was particularly severe among large mammals (over 100 kg; Faith and Surovell 2009). Researchers speculate that these megafauna may have had profound ecological effects (Johnson 2009), including serving as seed dispersers for many species of plants (Barlow 2001, Janzen 1982, Peterson 1991). Although North America still has a diverse assemblage of large mammals that could be potential seed dispersers, most survivors are either ruminants or carnivores. Today, there are no large, native, non-ruminant herbivorous mammals over most of the temperate portions of the continent (*Pecari tajacu*, L. [Collared Peccary] ranges into small parts of temperate North America). Ruminants, since they chew their cud and have a fermenting stomach, destroy most seeds they consume and are therefore likely poor potential seed dispersers (Barlow 2000, Cosyns et al. 2005, Prasad et al. 2006; but see Janzen 1982). Carnivores typically have guts designed to

¹Department of Biology, Hendrix College, 1600 Washington Avenue, Conway, AR 72032.

*Corresponding author - Moran@hendrix.edu.

rapidly process food and with harsh conditions to defend against pathogens (Janzen 1977, Rosenblatt et al. 2014, Stevens and Hume 2004), so while they occasionally supplement their diet with fruit, they may not be ideal seed dispersers. We suggest that large non-ruminant herbivorous mammals would have been much better Pleistocene dispersers, much as they serve that role in locations where they survive today (Donatti et al. 2007, Henry et al. 2000, Janzen and Martin 1982).

While it is impossible to assay the effects of extinct animals' digestion on seeds from anachronistic fruit, two formerly prominent and widespread North American mammals, *Mammot americanum* Kerr (American Mastodon) and *Equus* spp. (North American horse), have living analogs. *Elephas maximus* L. (Asian Elephant) is related (diverged about 27 million years ago; Shoshani et al. 2007), and therefore presumably physiologically and behaviorally similar to the American Mastodon (Aguirre 1969, Thomas et al. 2000). *Equus ferus caballus* L. (Domesticated Horse) was derived from Asian horse ancestors in recent times. That lineage diverged from the North American horse about 5 million years ago (Weinstock et al. 2005), has similar tooth morphology (Wang et al. 1994), and presumably still resembles its evolutionary relative in physiology and behavior (Janis 1976).

Some North American examples of proposed anachronistic fruit include *Diospyros virginiana* (L.) (American Persimmon), *Maclura pomifera* (Raf.) (Osage Orange), and *Asimina triloba* (L.) (Paw Paw). Researchers have argued that these fruits have characteristics—either 4–10 cm in length with up to 5 large seeds (American Persimmon and Paw Paw) or greater than 10 cm with numerous small seeds (Osage Orange) (Guimaraes et al. 2008)—that are adaptations for megafaunal dispersal (Barlow 2000). At the time of European settlement, these species appeared to have contracted ranges (Berry 1916, Burton 1990, Murphy 2001, Skallerup 1953), perhaps because they were not able to recolonize their former territory as the glaciers retreated at the end of the last ice age. Previous studies examined the ability of *Canis latrans* Say (Coyote) and *Procyon lotor* L. (Raccoon) to disperse American Persimmon and Paw Paw seeds (Cypher and Cypher 1999, Roehm and Moran 2013). Seeds collected from Coyote scat germinated at the same rate as whole fruit and dissected-seed controls but showed significant reduction in plant quality (Roehm and Moran 2013). Seeds ingested by Raccoons had significantly higher germination rates than controls (Cypher and Cypher 1999), but there was no measure of plant quality in that study. While researchers have speculated on potential seed dispersers for Osage Orange, and anecdotal evidence indicates horses may be dispersers (Schamback 2000), no direct investigations have been published addressing this species. We cannot completely discount, and it has been suggested, that human populations in North America selected for large fruits in more recent times (12,000 years ago to present; Peterson 1991), but there is little evidence for cultivation of these 3 species, and Osage Orange is not edible to humans.

In this study, we fed the 3 anachronistic fruits to Asian Elephants and Domesticated Horses and collected seeds from dung. We grew these collected seeds in a common garden experiment with appropriate controls and measured germination success, days to sprout, and plant quality.

Materials and Methods

Fruits from American Persimmon and Osage Orange were collected from the ground under several trees in Faulkner and Conway counties in central Arkansas during mid- to late October and late October, respectively (2012 and 2013 for American Persimmon: 35°08'46"N, 92°53'54"W and 35°08'09"N, 92°29'25"W; 2011 and 2012 for Osage Orange: 35°14'48"N, 92°28'25"W). Fruits of Paw Paw were purchased from Earthy Delights in Okemos, MI, in late September 2013. The fruits were fed to 2 female Asian Elephants on Riddle's Elephant and Wildlife Sanctuary in Guy, AR, and 2 Domestic Horses (quarter horse and thoroughbred mix) from a private ranch, also in Guy, AR.

For the American Persimmon experiments, 40 fruits were fed to each elephant on 2 separate occasions: 16 October 2012 and 31 October 2013. Twenty fruits were fed to each horse during a single trial on 31 October 2013. For the Osage Orange experiments, the elephants were each offered 1 Osage orange fruit on 25 October 2012 in a preliminary feeding trial to determine if they would eat the fruits. Anecdotal information (Schambach 2000) and personal observations had indicated that horses would consume Osage Orange fruit. For the official seed-collection experiments for Osage Orange, elephants were offered 2 fruits each on 29 October 2012, and the horses were offered 1 fruit each on 11 November 2011. For the Paw Paw experiment, we offered 15 fruits to each of the elephants and 10 to each of the horses on 27 September 2013, but none would consume the fruit. We attempted the Paw Paw feeding with 5 additional horses and 1 *Equus africanus asinus* L. (Donkey) on the same date. In all trials, we fed horses fewer fruits compared to elephants because of their smaller size and concerns for their gut sensitivity to unusual foods.

After feeding, both elephants and horses were kept in enclosures so that all their dung could be collected. We periodically removed the dung from the enclosures and searched it carefully to recover any intact seeds. Dung was collected for 54 hours, well past the average time for gut passage in elephants (Hackenberger 1987) and horses (Van Weyenberg et al. 2005). We monitored dung for an extended time (14 days) in the 2011 feeding trial of Osage Orange to horses. Intact seeds were removed and stored temporarily (i.e., less than 3 days) in the refrigerator at 3 °C. We then grew recovered seeds with appropriate comparison groups in a common garden experiment in a greenhouse. For the American Persimmon experiment, we established 4 treatments: 3 digested seeds per pot with 20 g of elephant dung (WD; $n = 26$), 3 digested seeds per pot without dung (WO; $n = 26$), 3 manually dissected seeds per pot controls (DS; $n = 30$), and whole-fruit controls (WF; $n = 55$). For the Osage Orange experiment, we established 3 treatments: one animal-digested seed per pot without dung (WO; $n = 94$), 1 manually dissected seed per pot controls (DS; $n = 50$), and whole-fruit controls (WF; $n = 5$). Because of the relatively small number of seeds recovered from the Osage Orange, the refusal of elephants to consume more fruits, and the subsequent limited amount of replication possible, we did not plant a treatment group with elephant dung. Seeds were planted 1 cm deep in 200-ml plastic pots filled with GardenPlus™ all-purpose potting soil. Because of their large size, the Osage Orange whole fruits were planted in 1000-ml pots. We consider whole fruit treatments to be the most natural in representing uneaten

fruits in the wild (Roehm and Moran 2013, Samuels and Levey 2005). However, the manually dissected seed controls are also important since these comparisons differentiate effects of digestion from effects of removal from fruit. Many fruits have growth inhibitors that delay sprouting (Robertson et al. 2006), so the manually dissected control removes that confounding variable. Since Paw Paw was not consumed by either herbivore, there were no further experiments performed with that species.

After planting, the pots containing American Persimmon and Osage Orange seeds and fruits were placed in a refrigerator at 3 °C for 60 days to cold-stratify the seeds, a requirement for both species to germinate (Burton 1990, Halls 1981). After cold-stratification, the seeds were placed in a greenhouse, watered as needed, and observed every day for 96 days. We determined germination success and emergence times using the first day that a sprout was observed above the soil. At the end of the experiment, the seedlings were cut at soil level, dried for 24 hours at 50 °C, and weighed to determine aboveground dry biomass. To determine whole-fruit treatment germination success, we dissected the fruits from the pots to measure how many seeds had not sprouted.

We analyzed germination success by chi-square analysis. Since the measure for the chi-square analysis was germination success (positive or negative) and some treatments had multiple seeds per pot, there was inevitable pseudoreplication. We calculated mean seedling emergence time and mass per pot to avoid pseudoreplication (although many seeds came from the same fruit, particularly the Osage Orange experiments) and then analyzed these data by one-way ANOVA, followed by a Tukey post-hoc test if significance was found.

Results

For the American Persimmon trials, both horses and elephants eagerly consumed the fruits. In the elephant trials, all but 1 fruit was consumed (one was dropped by the elephant and perhaps unnoticed), while in the single horse trial, all were consumed. From the estimated number of seeds in persimmon fruits (Roehm and Moran 2013), we recovered 36.4% of seeds fed to the elephants (126 of the 346 estimated number of seeds). Germination success was significantly affected by treatment, with elephants seeds planted in dung (WD), elephant seeds without dung (WO), and manually dissected seeds (DS) all sprouting at significantly higher rates compared to whole fruit (WF) controls (Table 1). No intact seeds were recovered from the horse trials, although we did recover numerous fragments.

Persimmon seeds that had passed through elephant guts had generally faster sprouting times than those that did not (one-way ANOVA: $F_{3,86} = 7.09$, $P < 0.001$;

Table 1. Proportion of seeds sprouting for two species of anachronistic fruits fed to elephants. WD = seeds with dung, WO = seeds without dung, WF = whole fruit control, and DS = manually dissected seeds control. Letters indicate significantly different groups

Species	WD	WO	WF	DS	χ^2	P
<i>Diospyros virginiana</i>	0.53a	0.54a	0.200b	0.61a	67.25	<0.01
<i>Maclura pomifera</i>	n.a.	0.18a	0.001b	0.63c	751.42	<0.01

Fig. 1A). Mass of the plants at the end of the experiment was not significantly different between treatments (one-way ANOVA: $F_{3,86} = 0.53$, $P = 0.63$; Fig. 1B), although there was a trend for lower final mass for the whole-fruit controls.

For the experimental feeding of Osage Orange, the 2 horses readily and eagerly consumed the fruit during the 2011 experiment. However, we recovered no seeds from the dung after monitoring the horses for an extended period (14 days), well past the expected time for gut passage. Compared to horses, elephants reacted differently to the Osage Orange fruit offerings. While both elephants consumed an Osage Orange fruit during the preliminary trial, they appeared much less interested in subsequent attempts. One elephant refused to consume the fruit at all while the second elephant consumed 3 fruit, though she appeared somewhat disinterested and required multiple offering attempts to convince her to ingest them. In further trials, neither elephant would consume additional Osage Orange fruits. From the one elephant that consumed the Osage Orange fruits, we recovered 94 intact seeds,

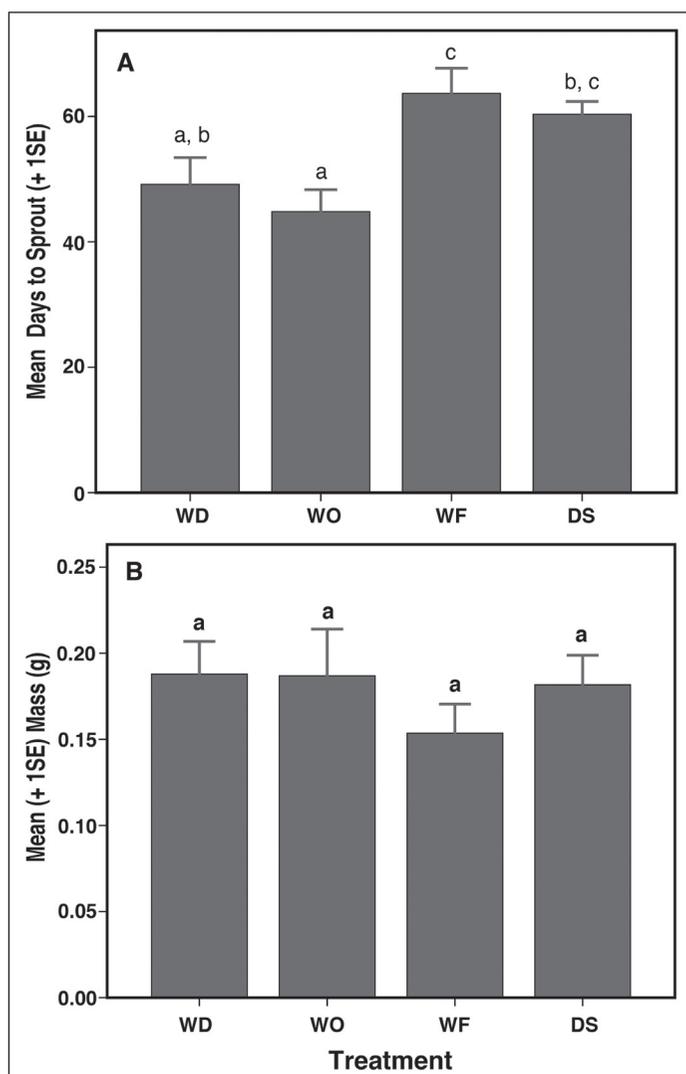


Figure 1. Effect of gut passage on (A) days to sprout and (B) seedling mass at the end of the experiment for the *Diospyros virginiana* (American Persimmon). Letters above bars indicate significantly different groups as determined by Tukey post-hoc analysis. WD = seeds planted with elephant dung, WO = seeds planted without elephant dung, WF = whole fruit control, and DS = manually dissected seed control.

which represents an estimated 11.1% recovery rate. Of these, only 18.1% sprouted, compared to 62.5% that sprouted in the manually dissected control treatment ($\chi^2 = 36.10$, $P < 0.001$). For the 5 whole fruits that were planted, only 2 seeds sprouted from the estimated 1542 seeds (Bonner and Karrafalt 2008), representing an extremely low germination success (Table 1). Osage Orange seeds that had passed through elephants and manually dissected seeds sprouted in the same amount of time (Fig. 2A) and had the same final mass (Fig. 2B). Whole-fruit controls took longer to sprout ($F_{2,65} = 21.36$, $P < 0.001$) and had lower mass ($F_{2,63} = 3.99$, $P = 0.023$), but since we only had two replicate sprouts for that treatment (because of extremely low germination success), this statistical result is of limited value.

Surprisingly, both elephants and horses refused to consume fruits from Paw Paw. Both elephants tasted the fruits, somewhat reluctantly, but immediately dropped them and refused to ingest them, even if put directly in their mouths. All 7 horses

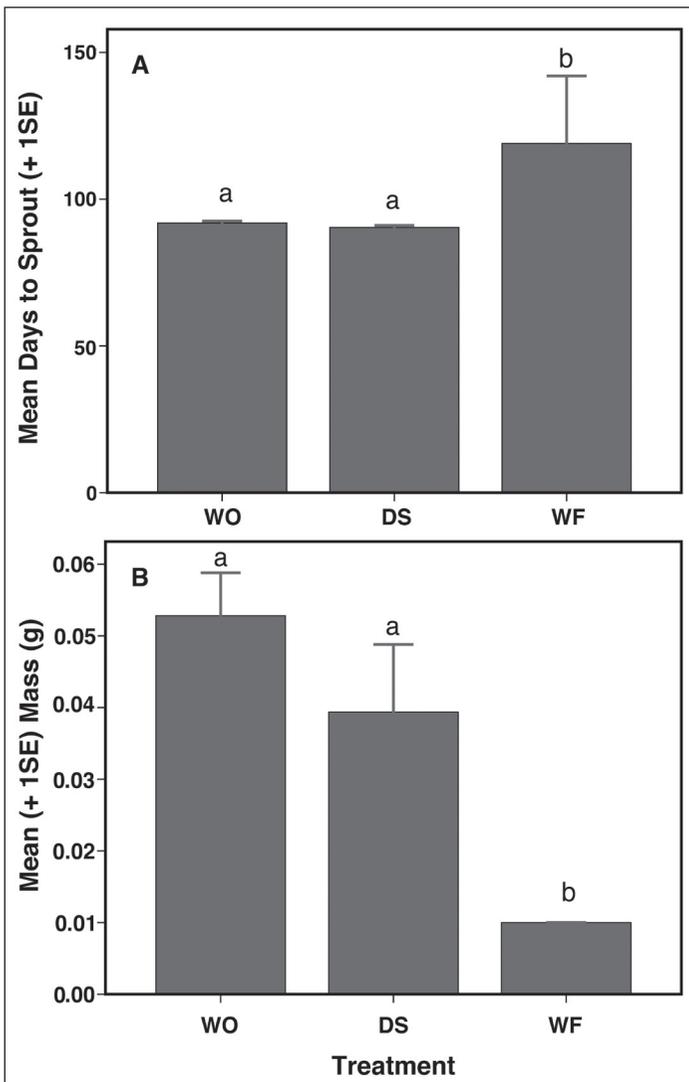


Figure 2. Effect of gut passage on (A) days to sprout and (B) seedling mass at the end of the experiment for the *Maclura pomifera* (Osage Orange). Letters above bars indicate significantly different groups as determined by Tukey post-hoc analysis. WO = seeds planted without elephant dung, WF = whole fruit control, and DS = manually dissected seed control.

and the 1 donkey eagerly attempted to consume the fruits but immediately dropped them, after which they refused any further attempts. They also exhibited the flehmen response after tasting the fruit.

Discussion

Our results indicate that the response of the seeds to ingestion depends upon the fruit species and potential disperser species. We recovered a substantial fraction of American Persimmon seeds from elephant dung. These seeds appear to be affected positively by gut passage through elephants in that they had higher germination success compared to whole-fruit controls. They also sprouted faster than both whole fruit and manually dissected control groups. Seedling quality, measured as mass of seedlings, was similar for all treatment groups. These results together suggest that elephant ingestion effectively removes seeds from fruits, releasing them from fruit inhibition (Robertson et al. 2006), without damaging the seedlings. These results differ from previous experiments with Coyotes (Roehm and Moran 2013), whose ingestion does not increase germination success and damages seeds. Racoons are also known to increase sprouting success (Cypher and Cypher 1999), similar to our elephant results, although their effect on time to sprout and plant quality is unknown.

The elephant results for Osage Orange differed from the persimmons. We recovered proportionally one-third as many intact seeds from elephant dung as compared to persimmons. Although the ingested seeds sprouted more successfully than whole fruits (which basically failed to sprout), they had much lower success compared to manually dissected seed controls. The time to sprout and seedling quality were almost exactly the same between elephant-ingested seeds and manually dissected controls. These results indicate that although it is important for the seeds to be removed from the fruit, which apparently inhibits germination, elephant passage damages the seeds severely enough that very few survive gut passage intact and even fewer sprout.

Although horses readily consumed American Persimmon and Osage Orange, the seeds of neither survived gut passage. Seed fragments were common in the dung samples, so we conclude that horses masticate their food more thoroughly than elephants. Some additional published evidence indicates that horses are particularly destructive to seeds when feeding on fruits (Janzen 1982). Horses are known to consume persimmons (Cummings et al. 1997), and anecdotal evidence indicates that horses are very fond of Osage Orange fruits (hence the common name “horse apple”; Schambach 2000). Authors have speculated that because of their apparent affinity for Osage Orange fruits, horses coevolved to become important dispersers (Barlow 2001). We observed that they indeed are very fond of the fruits, consuming them much more eagerly than elephants. However, based on our data, horses do not appear to be effective dispersers. Considering their destruction of all the seeds in our trials and their apparent morphological and behavioral similarity to extinct North American horses (Wang et al. 1994), we therefore suggest that Pleistocene horses were also poor dispersers of the plant species we tested.

Surprisingly, neither elephants nor horses would eat Paw Paw fruits. Both species tasted the fruits but refused to consume them. The horses exhibited a flehmen response, which although usually associated with sexual behavior, is also known to occur due to odors they find objectionable (Saslow 2002). This result was surprising given that Paw Paw fruits are known to be non-toxic and high in nutritional quality (Peterson et al. 1982), though there is some evidence the skin may have toxic compounds (Layne 1994). We currently have no explanation for the negative response to the fruits by both of our test species.

Our results suggest that North American Pleistocene proboscidians (e.g., American Mastodon) could have been important seed dispersers for the American Persimmon. The results also indicate possible coevolution, but results from living potential dispersers (e.g., Raccoon; Cypher and Cypher 1999) show that the plant did not necessarily coevolve exclusively with one disperser. This interpretation assumes that extinct North American proboscidians were similar in behavior and physiology to extant elephants. There is no opportunity to test this assumption directly, but published data indicate that the American Mastodon was a generalist, feeding by grazing and browsing (Green et al. 2005, Newsom and Mithlacher 2006), and had similar digestive function (Haynes 1993). Living elephants are known to target fruiting trees and are well-known seed dispersers in their native habitats (Campos-Arceiz and Blake 2011), further supporting our hypothesis. Mastodons almost certainly traveled long distances (Hoppe et al. 1999), which would have made them particularly good potential dispersers compared to living species (e.g., raccoon). Fossil remains of mastodon dung have contained evidence of the fruits and seeds of many species, including at least one instance of American Persimmon (Newsom and Mithlacher 2006).

It has been suggested that because of its extremely large size, fruit of Osage Orange coevolved exclusively with elephants (Barlow 2001). However, we do not find evidence in our experiments for that premise. Both elephants ate the Osage Orange fruits during the preliminary feeding trials but appeared less interested in them in further attempts (1 rejected them, and 1 ate them somewhat unenthusiastically). Few seeds survived gut passage and even fewer sprouted. Osage Orange fruits have an extremely large number of seeds, which some argue is an adaptation to ensure some seeds survive animal dispersal (Guimaraes et al. 2008), and indeed a small percentage did survive gut passage through the 1 elephant that would consume them. However, the fruits do not appear particularly palatable since they possess copious amounts of milky sap, a strong unpleasant smell, and a fibrous texture (Burton 1990). Conversely, the seeds are highly nutritious (Saloua et al. 2009), unlike those of persimmons and Paw Paw, which are protected with toxins (Vines 1960, Woo et al. 1999). Squirrels are known to feed heavily on the seeds of Osage Orange (Korschgen 1981), but they are probably not effective dispersers since they likely severely damage the seeds they eat and have not been observed caching any. We therefore suggest that the Osage Orange fruit may actually be a protective structure to deter herbivory and has not evolved to attract potential seed dispersers. How the seeds are ultimately dispersed from the parent plant remains a mystery.

This study is important for understanding the ecological and evolutionary relationships between extinct mammals and extant plant species. The high rate of recent

North American large-mammal extinctions but low rate of plant extinctions may have terminated numerous plant-animal interactions, with likely consequences for distribution and abundance patterns and ecosystem function. Various conservation groups have suggested a “rewilding” of temperate habitats across North America and Eurasia with ecological analogs (e.g., Asian elephant in place of the American Mastodon), and recent technological advances have even raised the possibility of “de-extinction” of Pleistocene mammals with the goal of eventual reintroduction to the wild. While there is much debate on the benefits and risks of such rewilding programs (Donlan et al. 2006), it seems likely that research teams will proceed if the technological hurdles can be overcome. If such experiments are undertaken, it will be important for ecologists to understand the potential interactions of these species with the native environment and how they will affect ecosystem function.

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