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Mesopredator frugivory has no effect on seed viability and emergence under experimental conditions

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Abstract. Members of the order *Carnivora* are a unique and important seed disperser who consume and deposit undamaged seeds while providing regular long-distance seed dispersal opportunities. Some members of *Carnivora*, such as coyotes (*Canis latrans*), are undergoing range expansions which may help the plant species they consume colonize new locations or replace dispersal services provided by recently extirpated species. In this study, we evaluated aspects of the seed dispersal effectiveness of coyotes and gut passage time to determine the potential dispersal distances for three commonly consumed and commonly occurring plant species (*Amelanchier alnifolia, Celtis ehrenbergiana*, and *Juniperus osteosperma*). We also investigated the potential effects of secondary dispersal of seeds away from scats by comparing seedling emergence from whole scats to those where seeds were first removed from scats. We found that seeds generally took between 4 and 24 h to pass through the digestive tract of coyotes, which could result in regular seed dispersal up to 7 km. Gut passage through coyotes had no effect on seed viability or emergence for any of the three plant species, including that gut passage for *A. alnifolia* and *J. osteosperma* does not replace cold stratification for breaking physiological dormancy. By simulating secondary dispersal, we found that 22% (±8.2%) more *C. ehrenbergiana* seedlings emerged when seeds were removed from scats and those seedlings emerged 7 d earlier (±5 d) compared to seeds that remained in the coyote scat. Coyotes are effective seed dispersers, with the potential for regular long-distance dispersal services and for providing opportunities for secondary seed dispersal, which could aid in climate migration or serve to replace extirpated dispersal mutualists.

Key words: *Canis latrans*; coyote; endozoochory; long-distance dispersal; migration.

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INTRODUCTION

Seed dispersal is necessary for sexually reproducing plant species to maintain gene flow and recruitment within a population and for migration and gene flow among populations (Levin et al. 2003, Levine and Murrell 2003). Dispersal aids in maintaining both plant community diversity and within-species genetic diversity, thereby improving community and species stability and persistence (Clobert et al. 2012). Additionally, dispersal improves the survival of individual propagules by moving them away from intraspecific competition or inhibition (Grubb 1977, Schupp and Fuentes 1995), specialized pathogens, and from predators that are attracted to an abundance of seeds and propagules immediately surrounding a maternal plant (Janzen 1970, Connell 1971, Comita et al. 2014). Seed dispersal also allows for the colonization of unpredictable or newly available habitats (Howe and Smallwood 1982). Effective seed dispersal occurs when quality seed (i.e., undamaged and viable) is deposited in quality locations (i.e., safe sites suitable for germination and growth) in sufficient quantities to ensure population establishment (Schupp 1993, Schupp et al. 2010). Thus, many species have adapted to utilize animals to increase the quantity of seeds transported in short- and long-distance dispersal through various mutualisms and commensalisms (Levin et al. 2003). Understanding the efficacy of these dispersal strategies and their mutualist or commensalist relationships is crucial to understanding and modeling seed dispersal.

Endozoochory is a form of seed dispersal that occurs via a mutualistic relationship with a vertebrate whereby the seed is transported inside the animal's digestive tract post-consumption. In many cases, seeds are covered with edible, fleshy fruit that promotes consumption by animals, which increases the quantity of seeds dispersed. Seed treatment by endozoochoric dispersers (e.g., mechanical damage during mastication; damage during digestion) can vary between different disperser and plant species and is an important aspect of the quality of seed dispersal effectiveness (Schupp 1993, Schupp et al. 2010, Perea et al. 2013). If seeds are unharmed, fruit consumption allows seeds to germinate after gut passage and feces deposition (Cypher and Cypher 1999, Steyaert et al. 2019). In some endozoochoric relationships, animal consumption of seeds can improve seed germination by removing fruit pulp, scarifying seed coats, and breaking physiological seed dormancy including for species that might otherwise require cold stratification (Traveset et al. 2007, Soltani et al. 2018).

Despite their name, many members of the order *Carnivora* [e.g., bears (*Ursus* sp.) and foxes (*Vulpes* sp.)] are highly omnivorous and consume large volumes of fruit, therefore providing substantial seed dispersal services (Rogers and Applegate 1983, Rosalino and Santos-Reis 2009, Lalleroni et al. 2017). The quantity and quality of seeds dispersed by *Carnivorans* make them a particularly important seed disperser in some regions. For example, *Carnivorans* in North America are considered the main mammalian seed disperser of all plant species (Willson 1993). Furthermore, *Carnivorans*' seed-laden scats are valuable resources for scatter hoarding, secondary seed dispersers, such as granivorous rodents (Enders and Vander Wall 2012, Shakeri et al. 2018). *Carnivorans* are important seed dispersers not only because they consume and deposit a substantial quantity of viable seeds, but they also have relatively large home ranges that can result in the long-distance dispersal of seeds (González-Varo et al. 2013, Herrera et al. 2016, Lalleroni et al. 2017). Long-distance seed dispersal is important for plant ecology and conservation because it facilitates gene flow among populations and the colonization of new areas (Falk and Holsinger 1991).

Coyotes (*Canis latrans*) are mesocarnivores that occur throughout most of North America and consume a wide variety of fruits (Kitchen et al. 1999, Roehm and Moran 2013). The generalist diets of coyotes allow them to take advantage of different prey items as they become available, including several seasonal fruits (Morey et al. 2007, Petroelje et al. 2013). Seeds deposited in natural ecosystems from coyote frugivory commonly result in neutral or increased germination (Schupp et al. 1997, Roehm and Moran 2013). However, the effects on some seeds can be negative (Cypher and Cypher 1999). Because results are generally neutral or positive, coyotes are hypothesized to be effective seed dispersers for many plant species. However, no controlled studies have investigated the effects of gut passage or gut passage time on seed viability and germination. Such information would improve our understanding of coyotes as effective seed dispersers and our ability to model seed dispersal by coyotes.

Coyotes are an interesting seed disperser because, unlike many frugivores, their range is expanding. Since the 1950s, coyotes have expanded their range by 40%, the largest expansion of any North American *Carnivoran* in the same period (Laliberte and Ripple 2003, Hody and Kays 2018). In the early 1900s, coyotes primarily inhabited the unforested western two-thirds of North America. Today, coyotes are found in taiga, deciduous, coastal temperate, and tropical forests from Canada and southern Alaska to Central America (Hody and Kays 2018). Because coyotes disperse viable seeds, their range expansion could be aiding in broader dispersal and colonization patterns of the plant species they consume. Additionally, in areas where coyotes are recent arrivals, they could be supplementing or replacing dispersal services previously carried out by species whose numbers have been reduced or have been extirpated entirely (Pérez-Méndez et al. 2016), as has been seen with other non-native *Carnivoran* species (Celedón-Neghme et al. 2013, Muñoz-Gallego et al. 2019). However, before we can understand the significance of coyotes as seed dispersers, we must first understand three key aspects of seed–coyote interactions: gut passage time (which influences how far a seed can be dispersed), its effect on seed viability, the rate and timing of germination, and the potential quantity of viable seeds dispersed.

This study had five main goals: (1) We measured gut passage time for three plant species (*Amelanchier alnifolia, Celtis ehrenbergiana*, and *Juniperus osteosperma*) from genera commonly consumed by coyotes (Schupp et al. 1997, Cypher and Cypher 1999, Dumond et al. 2001, Schrecengost et al. 2008). (2) We examined how gut passage through a coyote affects seed viability and seedling emergence of *A. alnifolia, C. ehrenbergiana,* and *J. osteosperma*. (3) We examined how diet composition may alter viability and emergence of *A. alnifolia, C. ehrenbergiana,* and *J. osteosperma*. (4) We also determined whether gut passage could break physiological seed dormancy for the two plant species in this study with physiological seed dormancy (which is often broken by cold stratification and sometimes scarification, *A. alnifolia* and *J. osteosperma*). (5) Finally, we experimentally evaluated the potential effect of secondary dispersal on quantitative and qualitative components of seed dispersal effectiveness. The results of this study are important for understanding the role coyotes play in seed dispersal.

METHODS

Seed selection

We identified 16 genera of plants with seed-bearing bodies consumed by coyotes (Schupp et al. 1997, Cypher and Cypher 1999, Dumond et al. 2001, Schrecengost et al. 2008). Three genera were identified that had distributions spanning the conterminous United States, were common within their respective geographic ranges, and had a subordinate species that were available from seed distributors or wild collection: Saskatoon serviceberry (*A. alnifolia,* 4–10 seeds per pome), desert hackberry (*C. ehrenbergiana,* 1 seed per drupe), and Utah juniper (*J. osteosperma,* 1–2 seeds per dry cone). *Celtis ehrenbergiana* and *J. osteosperma* both typically require cold stratification to break physiological seed dormancy (Baskin and Baskin 2014), allowing us to test if coyote gut passage could replace cold stratification in breaking dormancy. All three genera are woody taxa with wide spatial distributions (USDA & NRCS 2020), and at least *Juniperus* is already experiencing range expansion (Weisberg et al. 2007, Rowland et al. 2011), making them interesting models for evaluating *Carnivoran* consumption and dispersal potential. *Amelanchier alnifolia* and *C. ehrenbergiana* were both purchased as whole dried fruits from native seed distributors (Native Seed Company and Granite Seed, respectively). In contrast, *J. osteosperma* seed cones were collected from a wild population in Green Canyon near Logan, Utah, USA. Before feeding, the *A. alnifolia* and *C. ehrenbergiana* fruits were rehydrated to ensure consumption by coyotes and to emulate wild presentation.

Captive coyote trials and gut passage time

Captive coyotes housed at the USDA-National Wildlife Research Center's Predator Research Facility in Millville, Utah, USA, were fed 650 g of a high-protein, high-fat commercial food (Fur Breeders Agricultural Cooperative, Logan, Utah, USA) daily and provided water *ad libitum*. Coyote feeding trials took place between 20 June 2019 and 25 November 2019 and involved 20 coyotes. All coyotes were housed as male–female pairs in either 1000 or 10,000 m^2 outdoor enclosures but are regularly fed in a fixed location of equivalent size within each enclosure. Experimental feedings for this study included three diet ratio treatments: a control feeding (650 g of regular food), one-third seed-bearing body (217 g of fruit/cone and 433 g regular food, ˜2170 *A. alnifolia* fruits, 1670 *C. ehrenbergiana* fruits, and 800 *J. osteosperma* cones), and two-thirds seed-bearing body (433 g fruit/cone and 217 g regular food, ˜4330 *A. alnifolia* fruits, 3330 *C. ehrenbergiana* fruits, and 1600 *J. osteosperma* cones) for each of the three plant species. Two different proportions of seed-bearing bodies in feedings were used to determine whether diet composition altered gut passage time (Cipollini and Levey 1997) and the effect of gut passage on seed viability and germination due to differences in digestion with an increase in plant matter (Auger et al. 2002). We fed all coyotes their regular diet for a minimum of two days between experimental feedings. Each experimental feeding was mixed with a non-toxic glitter to allow for the identification of target scat after deposition (Burns et al. 1995). Although coyotes were housed as mated pairs, we fed them separately, and their food was mixed with different colors of glitter to enable the identification of scats to the individual. Twelve coyotes were fed for each treatment. Failure to participate occurred when a coyote refused to consume the experimental feeding or the coyotes ate from both feeding stations preventing individual ID of the resulting scats. All successful participants were observed until feeding concluded (feeding generally lasted 2–7 min) to establish gut passage start times. After each experimental feeding, the enclosure was checked after 4, 8, 24, and 48 h to establish gut passage time. All scats were collected and air-dried at room temperature to prevent mold formation before seed viability testing and emergence trials. All feeding trials were conducted under approval from NWRC's Institutional Animal Care and Use Committee (QA-3051).

Post-consumption seed viability testing

We blocked scats into groups by species of seed, the proportion of seed-bearing bodies in feeding, individual coyote, and time interval collected for viability tests post-consumption (Fig. 1). Scat was randomly selected from each block for seed viability testing if multiple scats were collected. The seeds were removed from each scat using water and by progressively sieving the scat with a starting mesh of 6.35 mm and a finishing mesh of 2.12 mm. If a scat failed to yield 100 seeds, it was discarded, and another one was randomly selected. This method was used for both *C. ehrenbergiana* and *A. alnifolia*.

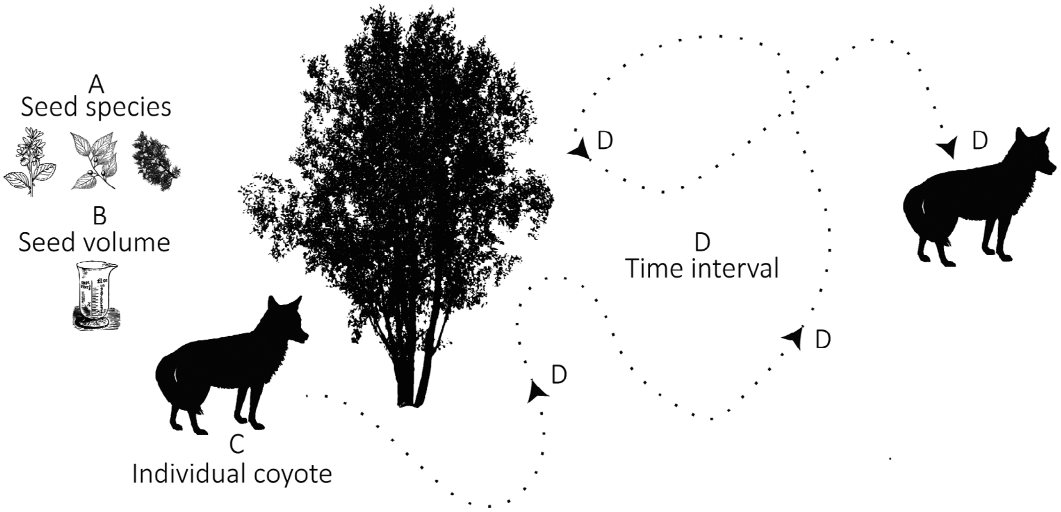

Fig. 1. Experimental design. Scat samples from captive coyotes fed seed-bearing bodies of three different plant species (*Amelanchier alnifolia, Celtis ehrenbergiana*, and *Juniperus osteosperma*) were blocked for post-consumption viability and emergence testing first by seed species (A) to detect any variation in species tolerance for gut passage and then by the proportion of the fruits/cones in the feeding by mass (B) to evaluate whether diet composition altered the effect of gut passage on seeds. Next samples were blocked by the individual coyote (C) to control for pseudoreplication and to detect any individual variation. Finally, samples were blocked by the post-consumption time interval (D) that they were collected to determine whether longer gut passage times and thus longer dispersal distances had an effect on seed viability or emergence.

No single scat yielded more than 50 *J. osteosperma* seeds; therefore, multiple scats from within the same block were randomly selected and combined to yield 100 seeds. To establish baseline seed viability, we tested three control samples of 100 seeds from the purchased *C. ehrenbergiana* and *A. alnifolia* seed lots and six control samples of 100 seeds from the wild-collected *J. osteosperma* due to its higher variability in viability. We followed the guidelines in the AOSA/SCST Tetrazolium Testing Handbook for seed viability tests (AOSA 2010). After being cut to expose the embryo, seeds were soaked for 18 h in a 1% tetrazolium solution at ~30°C. Then, the exposed embryo was inspected for the intensity of staining as relevant for each species (AOSA 2010).

Post-consumption seedling emergence testing

We randomly selected a scat from each block for seed emergence trials in a common garden experiment. Each selected scat was divided into half; seeds were removed from one half as described in the post-consumption seed viability testing section and the other half remained intact in the scat. Controls consisted of 100 seeds each for *C. ehrenbergiana* and *A. alnifolia*. A half scat from the *J. osteosperma* trials yielded approximately 25 seeds each and their seeds are quite large; thus, the controls were limited to 25 seeds so that the germination conditions were similar (e.g., seed density, distance from soil surface and vertical arrangement with other seeds) between the control and removal experimental samples. Removed seeds, intact scats with seeds, and controls were planted in a research greenhouse at Utah State University in Logan, Utah, USA. Whole scats were placed on the surface of the potting soil to replicate natural deposition, while removed seeds and control seeds were covered with potting soil to simulate scatter hoarding (Beck and Vander Wall 2010) and optimal germination conditions, respectively (Bonner et al. 2008). The greenhouse was maintained at 21°C, a temperature common in germination guidelines for all three species (Bonner et al. 2008, Beck and Vander Wall 2010). Supplemental lighting was provided to maintain a 12-h photoperiod. Samples were kept moist and checked for new emergence every 36–72 h. Emergence trials were run for 70 d (Bonner et al. 2008). The *A. alnifolia* and *J. osteosperma* seeds were not cold stratified to break seed dormancy (Bonner et al. 2008, Baskin and Baskin 2014) because we wanted to test whether or not gut passage would break dormancy for these species as has been observed in other species (Traveset et al. 2007, Soltani et al. 2018).

Data analysis

We ran linear and mixed effect models to test the effect of gut passage time and diet composition on seed viability, time to first emergence, and total number emerged while controlling for the variation in individual coyote gut passage times. Gut passage time and diet composition were both treated as continuous variables, with the mid-point of each collection interval being used for gut passage time (2, 6, 16, and 36 h, respectively). We also ran mixed effect models to evaluate the effect of varying fruit concentrations in the diet (one-third seed-bearing body versus two-thirds seed-bearing) on gut passage time. Finally, a pairwise t-test was run to compare days to first emergence and total emergence for removed seed samples and whole scats.

RESULTS

Of the 20 individual coyotes used in this study, between 10 and 12 individuals successfully participated in five of the six treatment diet combinations: 12 participated in the treatment of one-third seed-bearing body for *J. osteosperma*, 11 participated in both diet ratio treatments for *A. alnifolia,* and the one-third seed-bearing body treatment for *C. ehrenbergiana*, while only 10 participated in the two-thirds seed-bearing treatment for *C. ehrenbergiana*. The two-thirds ratio treatment of *J. osteosperma* failed to yield sufficient participation and samples because only five coyotes consumed this combination.

Gut passage time

A total of 484 scats were collected, 6% between 0 and 4 h, 20% between 4 and 8 h, 61% between 8 and 24 h, and 13% between 24 and 48 h for all treatments and the control (Table 1). Inclusion of seed-bearing bodies in the diet, the seed species, and feeding proportion did not affect average gut passage time (14.82 h, n = 484, SE = 0.96; Appendix S1: Table S1). We did not detect a

Table 1. The number of scats collected at each collection interval for each seed volume treatment and the control diet feeding, the number of samples from each treatment block, and control used in both tetrazolium testing (viability) and germination testing.

	One-third volume					Two-thirds volume						
Time interval	0–4 h	4–8 h	8–24 h	24–48 h	Total	0–4 h	4–8 h	8–24 h	24–48 h	Total	Control	No. of hours
Scat collection											10	0-4
A. alnifolia	3	8	71	6	88	3	21	45	19	88	29	4-8
C. ehrenbergiana	2	9	37	6	54	5	19	24	7	55	60	8-24
J. osteosperma	6	13	52	13	84	—	—	—	—	—	16	24-48
Total	11	30	160	25	226	8	40	69	26	143	115	
Viability testing												
A. alnifolia	—	5	10	3	18	—	8	11	3	22	3	
C. ehrenbergiana	—	1	9	1	11	—	7	7	2	16	3	
J. osteosperma	—	1	10	2	13	—	—	—	—	—	6	
Total	—	7	29	6	42	—	15	18	5	38	12	
Germination testing												
A. alnifolia	—	2	11	—	13	—	5	10	—	15	3	
C. ehrenbergiana	—	1	9	—	10	—	4	5	—	9	3	
J. osteosperma	—	1	6	2	9	—	—	—	—	—	3	
Total	—	4	26	2	32	—	9	15		24	9	

Notes: For tetrazolium testing, a sample was delineated by a single scat from its respective block for *Amelanchier alnifolia* and *Celtis ehrenbergiana* seeds and as a combination of scats from within the same sampling block for *Juniperus osteosperma* to reach a 100 seed sample size. All germination testing samples were single scats with varying volumes of seeds contained therein. The two-thirds ratio of *J. osteosperma* and the 0- to 4-h interval for all treatments failed to yield sufficient samples for viability and germination testing, and the *Juniperus* control required additional replicates due to higher variability in viability.

difference in gut passage time for individual coyotes (Appendix S1: Table S1).

Post-consumption seed viability

A total of 40 *A. alnifolia*, 27 *C. ehrenbergiana*, and 13 *J. osteosperma* samples consisting of 100 seeds each were tested for viability post-consumption (Table 1). Consumption and gut passage did not alter seed viability ratios compared to the control samples. An increase in the duration of gut passage ($\beta = 0.0$, $P = 0.54$) and diet ratios ($\beta = 0.04$, $P = 0.27$) similarly showed no significant change in seed viability ratios (Fig. 2; Appendix S1: Table S1).

Post-consumption seedling emergence

In total, 31 *A. alnifolia*, 22 *C. ehrenbergiana*, and 9 *J. osteosperma* samples were used for germination trials alongside three controls (un-digested seeds) of each species (Table 1). For all species, seedling emergence rates did not differ between the control and removed seed treatment. Seedling emergence was exceptionally low for the control and experimental treatments of *J. osteosperma* seeds (zero seeds emerged in control and experimental treatments) and *A. alnifolia* seeds (only one seed from an experimental treatment emerged and none from the controls), preventing further comparisons. The removed seed treatment, simulating secondary dispersal for *C. ehrenbergiana,* had a 22% ± 8.2% (95% CI) higher rate of emergence ($P < 0.001$, $n = 412/1765$ of removed seeds; $n = 136/2677$ of seeds in whole scats emerged), and first emergence was 7 d earlier (±5 d 95% CI, $P = 0.009$) compared to emergence from an intact scat. Diet ratio treatments and gut passage time did not affect the emergence ratio or the number of days to first emergence ($P \geq 0.1$; Appendix S1: Table S1).

DISCUSSION

Coyote range expansion and dietary breadth illustrate their potential for effective seed dispersal at both short and long distances. As coyotes expand their range, especially southward (Hody and Kays 2018), they are encountering an increasing number of fleshy fruited plants that have evolved for some level of endozoochory. Our results support the hypothesis that coyotes can act as effective seed dispersers for *Amelanchier*, *Celtis*, and *Juniperus* species. We found

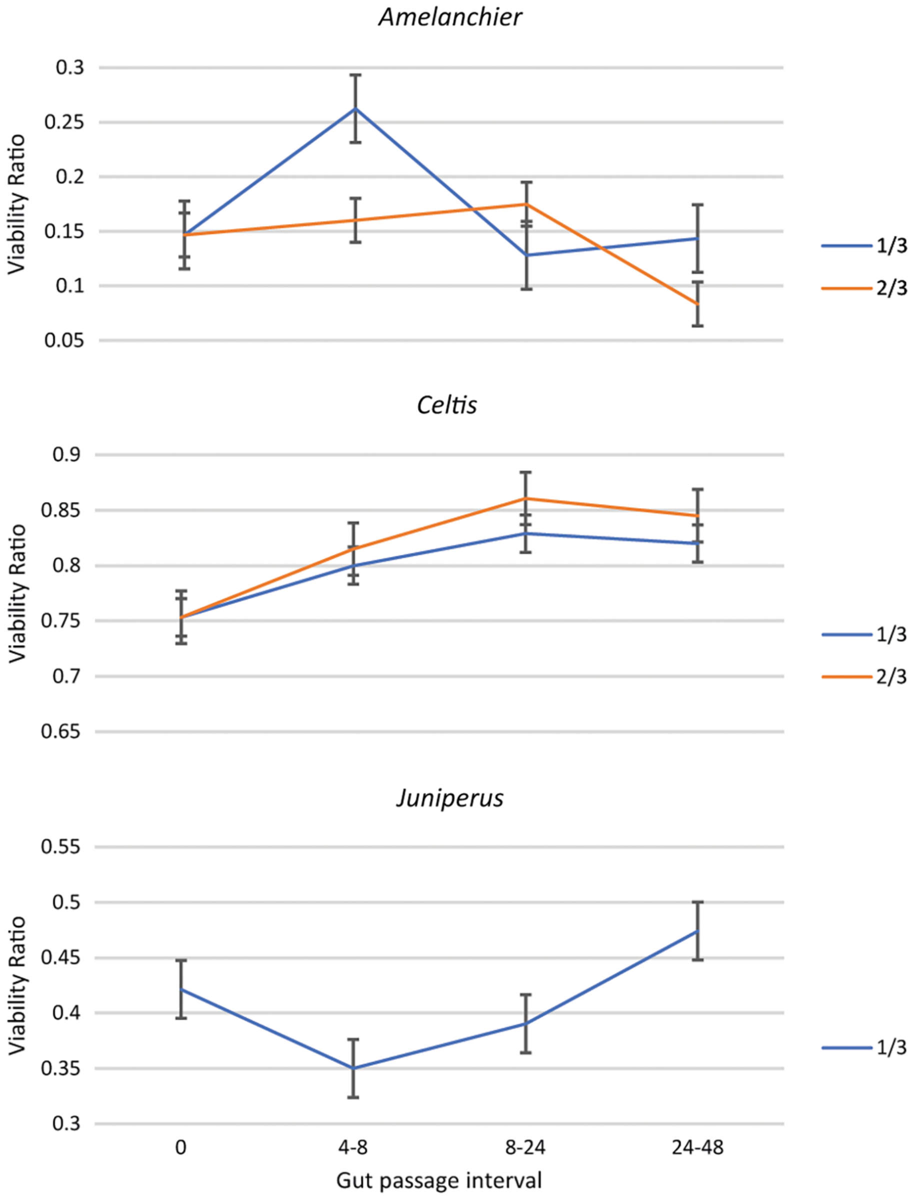

Fig. 2. Seed viability ratios. Captive coyotes were fed standardized feeding treatments consisting of a mixture of their regular diet of a high-protein, high-fat commercial food, and one-third and two-thirds seed-bearing bodies by mass, of three plant genera that their wild counterparts commonly consume (*Amelanchier alnifolia*, *Celtis ehrenbergiana*, and *Juniperus osteosperma*). Gut passage duration had no significant effect on seed viability for any of the species, nor did feeding composition for *A. alnifolia* or *C. ehrenbergiana* seeds (the two-thirds *J. osteosperma* treatment failed to yield sufficient samples for testing). All values are the mean of each treatment block with standard error bars around them.

no indication that consumption by coyotes or gut passage times affect seed viability of the three plant species studied. However, gut passage did not appear to improve seedling emergence for any of the plant species, and gut passage was not effective at breaking dormancy for *A. alnifolia and J. osteosperma* seeds, which typically require cold stratification. We also found that removing seeds from coyote scat improved seedling emergence speed and rate for *C. ehrenbergiana*, suggesting that secondary dispersal by scatter-hoarders may increase the quality of seed dispersal services by coyotes.

Current coyote diet patterns suggest that coyotes will consume any available fruit and, in turn, disperse their seeds (Kitchen et al. 1999, Roehm and Moran 2013). The establishment of novel mutualistic relationships is important for seed dispersal for two reasons. First, long-distance or atypical dispersal may be needed to help plants disperse to new locations that have recently become suitable because of climate change or anthropogenic land-use change (Corlett and Westcott 2013). Second, new dispersers can compete with native disperses or replace native dispersers that have been extirpated or are ecologically extinct (Celedón-Neghme et al. 2013, Pérez-Méndez et al. 2016, Muñoz-Gallego et al. 2019). If coyotes can play these roles, they may help maintain existing fruit-bearing plant populations by providing regular dispersal and genetic exchange or improving plant dispersal under changing climate conditions.

Amelanchier alnifolia, *C. ehrenbergiana*, and *J. osteosperma* seeds consumed by coyotes had average gut passage times between 4 and 24 h, with the majority being deposited more than 8 h post-consumption. Seeds that were deposited up to 48 h post-consumption had no reduction in viability. Although the two species that require cold stratification never emerged, *C. ehrenbergiana* seeds had no reduction in total emergence for any gut passage duration. Coyotes can regularly travel 7 km or more in 24 h (Young et al. 2006) and even average 0.94 km/h of net displacement (Kitchen et al. 2000) within home ranges of between 10 and 16 km^2 (Chamberlain et al. 2000, Gosselink et al. 2003, Gifford et al. 2017). All of these factors combined suggest that coyotes can provide more regular long-distance dispersal opportunities than other sympatric seed dispersers that may offer more irregular but longer distance dispersal (Escribano-Avila et al. 2014).

Our results support that coyotes are qualitatively effective seed dispersers, as our results show no negative effects on seed viability or emergence for all gut passage times and seed quantities. We were unable to test the qualitative effectiveness of deposition location in this study, but other studies have shown canids tend to deposit seeds in suitable locations for germination and recruitment (Escribano-Avila et al. 2014). As fairly prolific consumers of fruit (Kitchen et al. 1999, Roehm and Moran 2013), our findings also suggest coyotes are quantitatively effective seed dispersers. In this study, every consumption resulted in the deposition of viable seeds, even after extended gut passage times or high seed volume feedings. However, gut passage did not appear to improve seedling emergence for any of the plant species studied.

Two of the plant species used in this study, *A. alnfolia* and *J. osteosperma*, typically require cold stratification to break dormancy (Baskin and Baskin 2014). Plants dependent on cold stratification are particularly vulnerable in the face of climate change due to the additional niche requirement of sustained cold temperatures before germination (Poschlod et al. 2011). Previous studies have suggested that gut passage can aid in dormancy break for such species (Traveset et al. 2007, Soltani et al. 2018), making them less vulnerable to warming climates without needing to migrate as far from their current range. Our results found that coyote gut passage alone was not sufficient to break dormancy for either plant species. Thus, although coyotes may deposit viable seeds at farther distances than some other frugivores, our results suggest suitable habitats at the deposition site would still need to have prolonged cold periods to stimulate germination for these plant species. Thus, coyotes' long-distance dispersal services could be valuable for climate migration, but they do not appear to assist with local climate adaptation for *A. alnfolia* and *J. osteosperma*.

The quality of coyote seed dispersal improved when seeds were removed from scats by improving seedling emergence speed and rate. Seeds removed from scats had a 22% higher rate of emergence, suggesting that the scat's physical or chemical structure inhibited viable seeds from emerging. Additionally, large numbers of seeds deposited as a single scat may reduce seed dispersal quality due to inherent competition between seedlings if they are not spread out before emergence. Rodents regularly forage from the concentrated seed resource available in *Carnivoran* scats (Shakeri et al.

2018). The seeds collected by granivorous rodents are either immediately consumed, larder hoarded, or scatter hoarded (Beck and Vander Wall 2010). Consumption inherently reduces dispersal quality and quantity, and larder hoarding deposits seeds too deep for effective emergence, reducing dispersal quality (Beck and Vander Wall 2010). However, scatter hoarding deposits seeds in many different locations (increasing the quantity and diversity of dispersal locations) at depths that are more conducive to germination and emergence (Beck and Vander Wall 2010), essentially acting as gardeners planting seeds (increasing the quality of dispersal). Scatter hoarding is also the most common fate for seeds collected by granivorous rodents (Beck and Vander Wall 2010, Barga and Vander Wall 2013). Thus, secondary seed dispersal may improve the quality of coyote seed dispersal by increasing the quantity of dispersal locations from one to many and the quality of seed fate (increased emergence) in those locations. However, further studies examining the interplay between coyote seed consumption and secondary dispersers are needed.

Intraspecific variation of both the plant being dispersed and the dispersal mutualist is important to understand seed dispersal dynamics fully. Variation in plant characteristics, including fecundity, fruit, and crop size, can affect the qualitative and quantitative aspects of endozoochoric dispersal due to the quality of the seed itself or its attractiveness and availability for a high quantity of consumption (Schupp et al. 2019, Snell et al. 2019). Variation in disperser dominance, sex, behavior, and body size affects their access to seeds, travel distance during gut passage, and volume of seeds consumed (Zwolak 2018). This study utilized homogenized seed lots and controlled both feeding volume and access to the food in captive coyotes. Thus, using a highly controlled experimental population of coyotes limits any inferences we could make regarding intraspecific variation in gut passage time (which we did not detect) and its implications for potential dispersal distance. However, the controlled nature of this study allowed us to examine the effects of diet composition and gut passage time on seed viability and germination, which would have been very challenging to study using a wild population of coyotes.

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DATA AVAILABILITY

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.c.5324420.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3702/full