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Secondary Seed Ingestion in Snakes: Germination Frequency and Rate, Seedling Viability, and Implications for Dispersal in Nature

Gordon W. Schuett[1,2]*, Randall S. Reiserer[2], Andrew M. Salywon[3], Steven Blackwell[3], Wendy C. Hodgson[3], C. Drew Foster[4], James Hall[4], Ryan Zach[4,5], Mark A. Davis[6]* and Harry W. Greene[7,8]

[1] Department of Biology, Neuroscience Institute, Georgia State University, Atlanta, GA, United States, [2] Chiricahua Desert Museum, Rodeo, NM, United States, [3] Desert Botanical Garden, Phoenix, AZ, United States, [4] Arizona Center for Nature Conservation, Phoenix Zoo, Phoenix, AZ, United States, [5] Zoo Miami, Miami, FL, United States, [6] Illinois Natural History Survey, Prairie Research Institute, University of Illinois Urbana Champaign, Champaign, IL, United States, [7] Department of Integrative Biology, University of Texas at Austin, Austin, TX, United States, [8] Cornell University Museum of Vertebrates, Department of Ecology & Evolutionary Biology, Cornell University, Ithaca, NY, United States

Edited by:
Haldre S. Rogers,
Iowa State University, United States

Reviewed by:
Julieta Benitez-Malvido,
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Alex Karnish,
University of Arizona, United States

***Correspondence:**
Gordon W. Schuett
gwschuett@yahoo.com
Mark A. Davis
davis63@illinois.edu

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The importance of vertebrate animals as seed dispersers (zoochory) has received increasing attention from researchers over the past 20 years, yet one category in particular, diploendozoochory, remains understudied. As the term implies, this is a two-phase seed dispersal system whereby a secondary seed predator (carnivorous vertebrate) consumes a primary seed predator or granivore (rodent and bird) with undamaged seeds in their digestive tract (mouth, cheek pouch, crop, stomach, or other organ), which are subsequently eliminated with feces. Surprisingly, although snakes are among the most abundant predators of granivorous vertebrates, they are the least studied group insofar as our knowledge of seed rescue and secondary dispersal in a diploendozoochorous system. Here, using live snake subjects of the Sonoran Desert (one viperid and two colubrid species) and seeds of the Foothill Palo Verde (*Parkinsonia microphylla*), a dominant tree of the same region, we experimentally tested germination frequency and rate, and seedling viability. Specifically, to mimic rodents with seed-laden cheek pouches, we tested whether wild-collected *P. microphylla* seeds placed in the abdomen of thawed laboratory mice and ingested by the snakes would retain their germination viability. Second, we examined whether seeds exposed to gut transit germinated at a greater frequency and rate than the controls. While we found strong statistical support for our first hypothesis, both aspects of the second one were not significant. Accordingly, we provide an explanation for these results based on specific life-history traits (dormant and non-dormant seeds) of *P. microphylla.* Our study provides support for the role of snakes as important agents of seed rescue and dispersal in nature, their potential as ecosystem engineers, and crucial evidence for the investment of field-based studies on diploendozoochorous systems in deserts and other ecosystems.

Keywords: *Crotalus atrox*, Foothill Palo Verde, diploendozoochory, *Lampropeltis splendida*, *Pituophis catenifer*, reptiles, seed rescue, seed dispersal

INTRODUCTION

The significance of diverse seed dispersal systems to biotic communities, especially concerning the important role of vertebrate animals as dispersers (zoochory), has received increasing attention from researchers over the past several decades (Correa et al., 2007; Traveset et al., 2007, 2008, 2014; Schupp et al., 2010; Hämäläinen et al., 2017; Coughlan et al., 2019; Beckman et al., 2021). In the dispersal system termed endozoochory, seeds are directly consumed (e.g., by bears, primates, rodents, birds, or turtles) and later voided via regurgitation or defecation (Traveset et al., 2001, 2007, 2008; Steyaert et al., 2019). Endozoochory is prevalent in many vertebrate lineages, including freshwater fishes (Galetti, 2007), anuran amphibians (Silva and de Britto-Pereira, 2006; Hocking and Babbitt, 2014), a variety of nonavian reptiles (Blake et al., 2012; Reiserer et al., 2018; Valido and Olesen, 2019; Falcón et al., 2020), birds (Nathan et al., 2008; Heleno et al., 2011; Padilla et al., 2012; Baños-Villalba et al., 2017; Bartel et al., 2018; Blanco et al., 2018; Coughlan et al., 2019; Bravo et al., 2021), and both placental and marsupial mammals (Traveset et al., 2014; Jaganathan et al., 2016; Hämäläinen et al., 2017).

Diploendozoochory, possibly first documented by Darwin (1859), differs from endozoochory in that it is a two-phase seed dispersal system with several key players. In this system, a secondary (P2) predator (e.g., carnivorous vertebrate) consumes a primary (P1) seed predator (granivore) such as a rodent or bird with seeds in its digestive tract (e.g., mouth, cheek pouch, crop, and stomach) which are subsequently eliminated in the feces of P2 (Hämäläinen et al., 2017). In diploendozoochorous systems, when a secondary predator (P2) such as a rattlesnake subjugates and consumes a primary seed predator (P1) that has intact seeds in its cheek pouches (e.g., in our system, a heteromyid and geomyid rodent), the seeds are transported to the digestive tract of P2 and ultimately excreted. Consequently, some or all excreted seeds from P2 potentially survive this journey and germinate; thus, they can be viewed as "rescued" from P1 (post-dispersal seed predation, see Gong et al., 2015). Unlike endozoochory, our present knowledge of seed germination and the fate of dispersed seeds by P2 in diploendozoochorous systems is limited (Vander Wall and Longland, 2004; Hämäläinen et al., 2017; van Leeuwen et al., 2017). Nonetheless, with increased knowledge of the trophic behavior and ecology of carnivorous vertebrates that feed on granivores, the role of seed rescue and secondary dispersal appears to be non-trivial (Vander Wall and Longland, 2004; Hämäläinen et al., 2017; van Leeuwen et al., 2017; Pérez-Méndez and Rodríguez, 2018; Reiserer et al., 2018). Importantly, diploendozoochory can influence plant fitness in a number of ways including (a) seed transport, (b) altering the viability of transported seeds, and (c) changing the quantity of seeds that are dispersed (Hämäläinen et al., 2017; Saldaña-Vázquez et al., 2019; Rubalcava-Castillo et al., 2020). Accordingly, numerous avenues of inquiry remain to be investigated in diploendozoochorous systems which include diversity of species as agents of seed rescue and dispersal (Hämäläinen et al., 2017; Reiserer et al., 2018).

Among the terrestrial vertebrates, snakes are the least studied group with respect to seed rescue and secondary dispersal (Engel, 1997; Reiserer et al., 2018). This deficiency is somewhat perplexing and lacks a clear explanation given that they can be among the most abundant predators (high population densities and biomass per hectare) of seed-eating mammals (e.g., rodents) and birds in temperate and tropical regions (Klauber, 1972; Greene, 1997; Bonnet et al., 2002; King et al., 2018; Reiserer et al., 2018; Martins and Lillywhite, 2019; Henderson et al., 2021). And recent work on rattlesnakes indicates their potential importance as agents in diploendozoochorous systems (Reiserer et al., 2018). Specifically, in a museum study of 50 preserved rattlesnake specimens, nearly 1000 seeds were found to be indirectly ingested by way of consuming rodents possessing seed pouches, particularly heteromyids and geomyids. Careful examinations of entire digestive tracts revealed that not only were rodent-derived seeds abundant, but that numerous seeds germinated in the snakes' colons (Reiserer et al., 2018).

In North America, geomyid, heteromyid and some sciurid rodents have specialized cheek pouches for transporting seeds from plant source to cache sites, where they are often eliminated from the pool of plant propagules by consumption (Price et al., 2000; Kaufman et al., 2004; Hope and Parmenter, 2007). However, in some cases, seeds stored in these caches will germinate after a rainy season. Distances for seed dispersal in scatter-hoarding mammals (Morris, 1962) vary greatly and depend on species, size of seeds, nutrition value, season, and a host of other factors. For example, kangaroo rats, species with cheek pouches (heteromyids), typically predate, and cache seeds close to their home burrow systems (Jones, 1989; Daly et al., 1992; see Price et al., 2000; Lichti et al., 2017; Wang and Cortlett, 2017). Lifetime dispersal distances in Merriam's kangaroo rat (*Dipodomys merriami*), a common rodent in the Sonoran Desert, range from 0 to 265 m in males, and from 0 to 158 m in females (Jones, 1989).

Seed-laden rodents are commonly consumed by snakes as they forage, but unlike raptors, coyotes, bobcats, and other endothermic predators which eat rodents and are known (or implicated) to be secondary seed dispersers (Sarasola et al., 2016), the role of snakes in seed dispersal in nature remains unexplored (Reiserer et al., 2018). Nevertheless, desert-dwelling rattlesnakes and other vipers can be abundant (e.g., western diamond-backed rattlesnake, *Crotalus atrox*, more than 50 adults per km^2), and individuals are capable of consuming 12–20 rodent meals and potentially hundreds of seeds (Vander Wall et al., 1998) during an active season lasting 25–30 weeks. Moreover, individuals occupy large home ranges in which they sometimes travel more than 2 km within several days (Beaupre, 2016; Schuett et al., 2016; DeSantis et al., 2020). Consequently, vast numbers of seeds may potentially achieve exceptionally long secondary dispersal distances, perhaps several times greater than those distributed by the rodents themselves (Nathan et al., 2008; Wang and Cortlett, 2017). Despite the importance of the findings by Reiserer and colleagues (Reiserer et al., 2018) and the potential of snakes as seed dispersers outlined above, the most crucial ecological and evolutionary corollaries of this system hinge on the survival of voided (excreted) seeds and viability of seedlings (Hämäläinen et al., 2017).

Here, using live snake subjects, we experimentally tested germination properties in seeds of the Foothill Palo Verde (*Parkinsonia microphylla*), an ecologically important and

FIGURE 1 | Western Diamond-backed Rattlesnake (*Crotalus atrox*). New Mexico SR 9, near Animas, Hidalgo County, New Mexico. Photograph courtesy of William Wells.

dominant tree of the Sonoran Desert (Bowers, 1994, 2004). We first tested whether wild-collected seeds of *P. microphylla* placed in the abdomen of thawed laboratory mice and ingested by viperid and colubrid snakes would germinate and produce viable seedlings. Specifically, in our primary study, we tested the Western-Diamond-backed Rattlesnake, *Crotalus atrox* (**Figure 1**), a pitviper (viperid) species, based on results of a previous study (Reiserer et al., 2018). In a secondary study, we tested two species of sympatric colubrid snakes in which seed rescue and consumption are unknown but predicted to be present based on their diets, the Desert Kingsnake, *Lampropeltis splendida*, and the Sonoran Gopher Snake, *Pituophis catenifer affinis* (**Figure 2**). Second, in the primary study only, we tested whether the seeds exposed to gut transit germinated at a greater rate and frequency than those of the controls, viz. the accelerated germination hypothesis (Castilla, 2000; Traveset et al., 2001; Hämäläinen et al., 2017; Hanish et al., 2020; Salazar-Rivera et al., 2020; Yang et al., 2021).

MATERIALS AND METHODS

Selection of Plant Species

The Foothill Palo Verde (*Parkinsonia microphylla*), the State Tree of Arizona[1], was selected for this study for several reasons. First, detailed information on its biology and life-history is widely available, including details on germination under natural and artificial conditions (Benson and Darrow, 1981; McAuliffe, 1986, 1990; Bowers, 1994, 2004; Bowers and Turner, 2002; Medeiros and Drezner, 2012). Second, the seeds are reasonably large (several mm across) and easily manipulated for the experiments we executed. Third, wild heteromyid and geomyid rodents (seed predators) are known to harvest the seeds of *P. microphylla*, temporarily storing them undamaged in their external cheek pouches and subsequently cache them below the soil surface, such as in burrows (McAuliffe, 1990; G. Schuett, pers. observ.). Furthermore, both of these rodent groups are common prey species of snakes from the Sonoran Desert, including the rattlesnake species (*Crotalus atrox*) and colubrid species (*Lampropeltis splendida* and *Pituophis catenifer affinis*) used in this study (Schuett et al., 2016; Reiserer et al., 2018; see **Supplementary Figure 1**). Last, Foothill Palo Verde is one of the most widely distributed and abundant trees of the Sonoran Desert (Arizona and northern Mexico) and its seeds are easily harvested (Bowers, 2004).

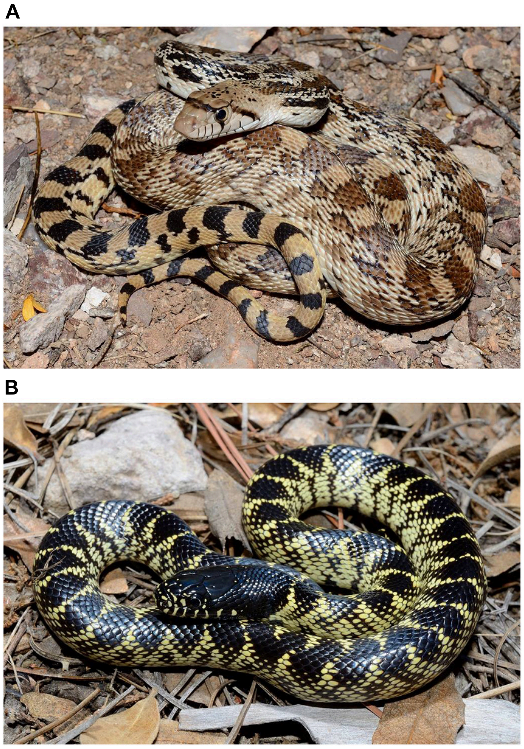

FIGURE 2 | (A) Sonoran Gophersnake (*Pituophis catenifer*). Vulture Mine Road, Maricopa County, Arizona. **(B)** Desert Kingsnake (*Lampropeltis splendida*). Animas Road, Hidalgo County, New Mexico. Photographs courtesy of William Wells.

Experimental Protocol

Though there are many approaches to reveal the impacts of digestion on seed germination and seedling viability (e.g., Guillen et al., 2009; Benítez-Malvido et al., 2014; Gonzalez-Di Pierro et al., 2021), few studies have assessed these metrics in diploendozoochorous systems, and none have examined them in snake species. We, therefore, developed a novel approach in which seeds of *P. microphylla* for this study were collected locally (Phoenix, Maricopa County, Arizona) from mature pods of a single tree in late June 2019. In most seeds, both germination frequency and rate are dependent on numerous factors (Mitchell et al., 2017), including genetic diversity within (Hantsch et al., 2013) and among populations (Ginwal and Gera, 2000; Donohue et al., 2005). Accordingly, to explicitly decouple these aspects of germination from potential genetic effects, we chose to

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[1] http:aznps.com/arizona-state-tree

select seeds from a single source tree. The study was divided into two treatments conducted at two different locations. The primary treatment group was conducted at the Chiricahua Desert Museum (Rodeo, Hidalgo County, New Mexico) and involved using the Western Diamond-backed Rattlesnake, *Crotalus atrox,* Trials involving the secondary group were conducted at the Desert Botanical Garden. The Phoenix Zoo and involved using the Desert Kingsnake (*Lampropeltis splendida*) and Sonoran Gopher Snake (*Pituophis catenifer affinis*).

The primary study (Chiricahua Desert Museum) used two Western Diamond-backed Rattlesnake, *Crotalus atrox* (**Figure 1**), collected as juveniles in Cochise County, Arizona as neonates (summer 2017), and reared individually to adulthood (1 m in total length at time of testing, 2019–2020). We followed standard institutional protocols for housing and husbandry for these two venomous snake species (e.g., Warwick et al., 1995; Smith, 2005). Five trials per snake (10 trials in total for both snakes) were carried out on the same day from December 2019 to April 2020. In each trial the two snake subjects were fed thawed (frozen) laboratory-reared mice (40 g) obtained from a common source that were impregnated with seeds of *P. microphylla*. Specifically, seeds for the treatment and control groups were randomly selected from a common source (∼1000 seeds). For each of the treatment trials, a total of 10 seeds (5–7 mm length) were used; five seeds were placed in the abdominal cavity in each of two adult commercial white laboratory mice (40 g each) that had been thawed. Owing to restrictions and difficulties of using wild heteromyid or geomyid rodents to feed snakes at our respective institutions (e.g., potential of disease transmission; availability of appropriately sized rodents), we lacked a rodent model with cheek pouches as vehicle for intact seeds. To mitigate this problem, we used a simple method to act as surrogate to the rodent cheek pouch: a small (1 cm) incision was made at the mid-venter of each thawed lab-reared mouse; five randomly selected seeds were inserted by hand and pushed gently just beneath the skin in the abdominal cavity; the incision was then lightly pinched to prevent seeds from being expelled during ingestion by the snakes. Both snake subjects were then promptly hand-fed two seed-impregnated mice. Each snake was observed during feeding until both mice were consumed. Hence, by coupling intact seeds with the body of the rodent, we experimentally mimicked the way seeds are handled by mice in nature. Since our main goal was to test for germination viability (performance) of snake-ingested foothill palo verde seeds (*P. microphylla*), the rodent was the natural vehicle for the seeds. Thus, whether test seeds were located in cheek pouches or just beneath the abdominal skin (abdominal cavity) of the ingested rodent, the fate of the seeds remains the same in being readily exposed to the digestive processes of the test snakes. No meal was refused by the snakes during the 5-month period of testing (December 18, 2019 to April 31, 2020).

Typically, the snakes had their first defecation within 5–7 days after ingesting the two mice implanted with seeds; a second defecation occurred up to 14 days after the treatment meal. Snakes were checked 3–4 times daily to obtain seeds as quickly as possible after defecation. Wastes were carefully removed from the cages and placed into a fine metal wire strainer. Tap water was gently run to help separate the seeds from the wastes (feces and urates). All harvested seeds were placed onto damp paper toweling before being incubated for germination tests. Five control trials, each with a total of 10 seeds (total of 50 seeds), were set up the same day (within 60 min) as the snakes were fed their treatment meal. None of the control seeds were scarified or altered in any way.

Seed Germination Protocol – Treatment and Control Groups

The *P. microphylla* seeds harvested from the feces of *C. atrox* were placed on damp paper toweling inside a plastic germination box. Each box was 28 L × 18 W × 13 H cm and had three small (7 mm) holes drilled on each side for air circulation. Furthermore, the seeds were covered with a single layer of wet (damp) white paper toweling (no dyes). The paper toweling and seeds were never allowed to become dry. The germination boxes were placed on a commercial rack equipped with 5 cm wide heat tape at one end. Each rack could hold 10 boxes. One end of each germination box was exposed to heat tape (28–30°C), which was set by an electric timer for 12D:12N. The seeds were never exposed directly to the heat tape. Air temperature inside the box during the day (12 h) was 26–30°C. During night, when the heat tape was off, air and substrate temperature was 21–24°C. Seeds used for the control trials were set up in different boxes, but were identical in all other respects to the treatment group.

The treatment and control groups of the primary study were checked 3–4 times daily for evidence of germination. Once seeds became imbibed (e.g., larger and paler in color than their original state), germination was imminent (hours). A seed was scored as germinated when a radicle was visible. Although the overall study was conducted from December 18, 2019 to August 31, 2020, a total of 257 days, each trial was allowed to run for approximately 4 months (128 days) for balance. Owing to diversified germination behavior (dormant and non-dormant seeds) in this species (Bowers and Turner, 2002; Bowers, 2004), this amount of time allotted for germination was deemed to be sufficient. For the treatment group, germination (days) was calculated as the period from the day of feeding until the appearance of the radicle.

Seedling Viability

To determine whether the germinated seeds of *P. microphylla* in the primary study would show seedling viability, multiple germinated seeds from each of the five treatment (snake-1: $n = 19$; snake-2: $n = 12$) and control trials ($n = 14$) were sown in small pots with commercial soil and allowed to grow to approximately 13–15 cm in height. The remaining germinated seeds were preserved in 95% EtOH. Germinated seeds in the secondary study were not tested for seedling viability.

Statistical Analyses

To test hypothesis 1, we used a binomial linear regression with germination (0 = no germination and 1 = germination) as the response variable, and treatment (snake digested and control), trial (first or second), snake (1 or 2), and defecation as explanatory variables. To test hypothesis 2, we used the non-parametric Mann-Whitney *U* test, as data were non-normally distributed, with time to germination (in days) as the response variable and treatment (as above) as the explanatory variable. The first analysis was conducted in R (R Core Team, 2021) in R Studio (R Studio Team, 2019), and the second using the open-source project JASP (Love et al., 2019)[2].

Secondary Study

Our secondary study using *P. microphylla* seeds was executed using two species of nonvenomous colubrid (colubrine) snakes, the Sonoran Gophersnake, *Pituophis catenifer,* and the Desert Kingsnake, *Lampropeltis splendida* (**Figure 2**). Both species are inhabitants of the Sonoran Desert and sympatric with the Western Diamond-backed Rattlesnake, *Crotalus atrox* (**Figure 1**). To our knowledge, there are no publications on seed rescue and germination in colubrid snakes. Importantly, as adults, both colubrid species consume similar mammalian prey (e.g., heteromyid and geomyid rodents) as the Western Diamond-backed Rattlesnake, *C. atrox* (Holycross and Mitchell, 2021).

Trials consisted of using two species of the two colubrid snakes (as above) and the same set of seeds collected for the primary study. Snakes were maintained at The Phoenix Zoo (PZ) as part of their public outreach collections. Owing to close proximity (1.6 km) seed germination was overseen at the Desert Botanical Garden (DBG). Three trials were run: the first was from August 23 to September 03, 2019 (11 days); the second was from October 1–28, 2019 (27 days); and the third was from March 1 to June 4, 2020 (95 days) Feeding of snakes at PZ was conducted as in the primary study, but only five seeds per feeding were used instead of 10. Snakes were checked once daily for voided excreta (feces and urates) and seeds. Excreta were placed in small plastic tubes (**Supplementary Figure 2**) and transferred to the DBG (1.6 km) for germination trials. In cases where the germination tests could not be started immediately, the samples were refrigerated at 1°C until use with 24–48 h. In trials 1 and 2, the seeds were not removed from the excreta before initiating germination tests. This was done to determine if any compounds in the excreta itself inhibit or promote germination and subsequent growth. The seeds used in the third trial were gently removed from excreta and briefly washed with tap water, similar to the trials in the primary study.

All seeds (in excreta or washed) were placed on Whatman® qualitative filter paper, Grade 1, 90 mm (Sigma-Aldrich, Inc., St. Louis, MO, United States) inside a plastic petri dish and moistened with distilled water. The petri dishes were then placed into a Percival 36-L germination chamber, model GR36L (Percival Scientific, Inc., Perry, IA, United States) with a schedule of 12 h day/12 h night, 25°C day /15°C night, and 75 micromole light intensity.

RESULTS

Primary Study (Chiricahua Desert Museum)

In the primary study, each trial in the treatment and control groups was 128 days. Excreted seeds of *P. microphylla* successfully germinated (**Figure 3**). Specifically, in the treatment group (five trials for each of the two rattlesnake subjects), 94 of 100 seeds (94%) were recovered from the feces; 78 (83%) of those successfully germinated (**Table 1**). Mean gut-passage time of seeds was 6 to 14 days (9.1 ± 2.5 days), and in eight instances germinated seeds were recovered in snake feces, implicating germination occurred during gut transit (sensu

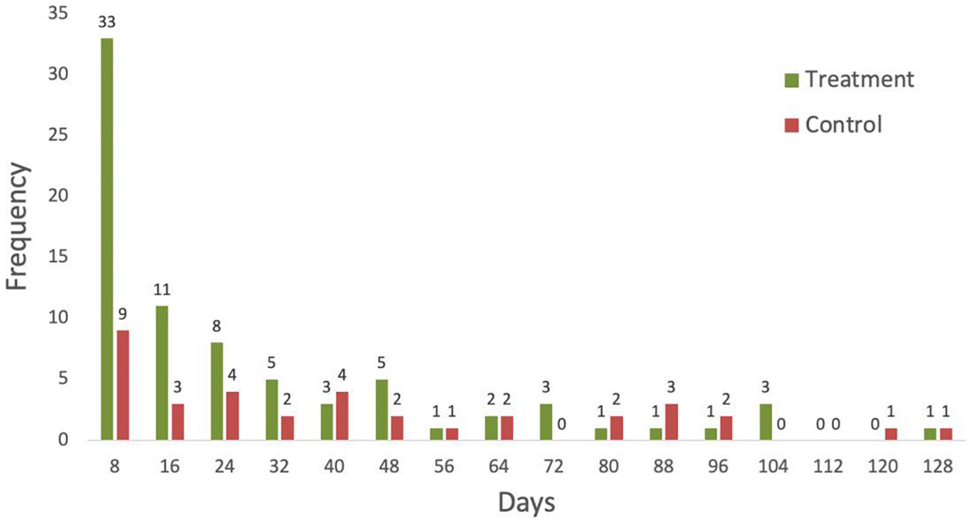

FIGURE 3 | Summary of germination frequency of *P. microphylla* seeds in the primary study involving the rattlesnakes (*Crotalus atrox*). Five trials were conducted and each one lasted 128 days. Germination (days) was calculated as the period from the day of feeding until the appearance of the radicle. The histogram was generated using the Histogram function in Excel version 16.48 Data Analysis Tool.

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[2] jasp-stats.org

TABLE 1 | Seed counts of *P. microphylla* in trial conditions of the primary study involving the Western Diamond-backed Rattlesnakes (*C. atrox*).

Trials	Initial sample	Unrecovered from scat	Ungerminated	Germination frequency
Control	50	–	14	36/50 (72%)
Treatment	100	6	16	78/94 (83%)

Reiserer et al., 2018). All seeds in preparation of germination (i.e., appearance of the radicle) became imbibed, swelling to twice their original size (11–13 mm length) and were noticeably paler in coloration (**Figure 4**). Of the 16 treatment seeds that did not germinate, 2 developed mold, yet the remaining 14 were normal in appearance and thus likely were viable (Bowers, 2004). In the control group (five trials), 36 of 50 seeds (72%) successfully germinated; 2 of the 14 ungerminated seeds developed mold yet the remaining 12 appeared to be viable. No significant differences were found in germination frequency with respect to any of the explanatory variables (i.e., treatment, trial, snake, and/or defecation) (**Table 2**).

Over the full duration of the experiment (128 days), mean germination time (GT) for treatment seeds was 31.9 days (SD: ± 27.2 days; min-max: 6–112 days) and 40.56 days (SD: ± 36.3 days; min-max: 2–123 days) for control seeds. No significant difference in GT was found between the treatment and control groups (Mann-Whitney *U* test: $U = 1465.5$, $p = 0.626$, ns) (**Figure 5**). All germinated seeds ($n = 45$) that were planted (treatment: $n = 31$; control: $n = 14$) from the primary treatment group survived and were grown to a height of 13–15 cm (**Figure 6**).

FIGURE 4 | Seeds of *P. microphylla* post-gut transit and recovered from feces of a rattlesnake (*C. atrox*) in the primary study. The seed on the left has undergone imbibition (imbibed and swelled) and germinated (presence of the radicle) while the other seed shows no outward change in appearance from its original state despite having been exposed to the digestive tract.

TABLE 2 | Logistic regression results from primary study.

Coefficients	Estimate	Std. Error	*Z*-value	*a*
Intercept	2.56E+00	1.38E+00	1.853	0.0639
Treatment	−9.42E-01	1.34E+00	−0.705	0.4808
Trial	−7.52E-02	1.59E-01	−0.474	0.6356
Snake	1.15E-15	5.78E-01	0.000	1
Defecation	−3.35E-01	5.82E-01	−0.575	0.5652

Testing whether or not seeds germinated with Treatment (snake digested or control), Trial (1 or 2), and Snake (1 or 2) as explanatory variables. With an alpha level of 0.05, all factors were non-significant, suggesting that snake-digested seeds were as viable as non-digested seeds.

Secondary Study (Desert Botanical Garden, the Phoenix Zoo)

The three trials yielded 22, 23, and 17 excreted seeds, respectively, from both snake species, and tests for germination ran for 11, 27, and 95 days, respectively. Five untreated seeds were used as controls for each of the three trials. A total of 16 seeds germinated after passing through the digestive tracts of the Sonoran Gophersnake (4 of 17 = 17.4%) and Desert Kingsnake (12 of 29 = 41.4%). Comparing trials 1 and 2, in which the feces containing the seeds were placed in the petri dishes, vs. trial 3, where seeds were removed from the fecal bolus and washed with tap water, revealed a large difference in germination frequency. Germination for the combined trials 1 and 2 were 15.6% (7/45) vs. 53% (9/17). Mold was an issue in many cases in the combined trials (**Supplementary Figure 3**), but far less so in trial 3 where the seeds were gently washed in tap water. Mold was rarely observed in the primary trials (see main text). The combined results of the three secondary trials revealed that the germination rate of the treatment seeds (16/62 = 25.8%) was not significantly different (7/25 = 28%) (Z-test, two-tailed: $Z = -0.210$, $p > 0.05$, ns) from the control seeds.

DISCUSSION

The most important outcome in all diploendozoochorous systems, from ecological and evolutionary perspectives, is that seeds survive all steps of the process—harvested or swallowed by a seed predator, swallowed whole or stored undamaged (e.g., cheek pouches and crop), swallowed undamaged by a secondary predator, and retention of germination viability after elimination from the gut of the secondary predator (Traveset et al., 2008, 2019; Hämäläinen et al., 2017). In a study involving preserved museum specimens of rattlesnakes (Reiserer et al., 2018), seeds found in the guts of snakes were derived from heteromyid and geomyid rodents, which were likely harvested and stored unharmed in their seed pouches. Uniquely, rattlesnakes and most other snake species subjugate and consume these rodents whole and do not chew (crush); consequently, most seeds transmitted through the GI tracts of snakes from these sources do not appear to be mechanically damaged. Furthermore, owing to long retention times in the digestive tracts of rattlesnakes, some seeds are capable of germination during gut transit (Reiserer et al., 2018; see Cabral et al., 2019; Carbajal-Márquez et al., 2020).

In support of our main hypothesis, we provide the first experimental evidence, to our knowledge, that seeds of the Foothill Palo Verde (*P. microphylla*) retain germination performance (e.g., viability) when indirectly consumed by

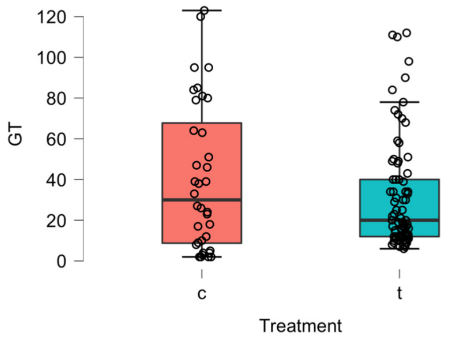

FIGURE 5 | Results of the primary study involving Western Diamond-backed Rattlesnakes (*C. atrox*). Box plots of mean germination times (GT - days) of *P. microphylla* seeds for control (c) and treatment (t) groups for 128 days. Horizontal line in boxes = median. Mann-Whitney *U* test: *U* = 1465.5, *P* = 0.626, ns.

FIGURE 6 | Examples of *P. microphylla* seedlings derived from the treatment group (snake gut transit) in the primary study involving Western Diamond-backed Rattlesnakes (*C. atrox*).

snakes—one species of rattlesnake and two species of colubrids—and subsequently recovered from their excreta (**Figures 1**, **2** and **Table 1**). Importantly, seeds found to be imbibed and germinated in excreta (feces/urates) produced healthy seedlings (**Figure 6**). In the primary study, all germinated seeds subsequently tested for seedling viability grew normally and developed into healthy plants.

Under the conditions of the primary study, both aspects of our second hypothesis (accelerated germination) were not statistically supported. The mature seeds of *P. microphylla* (located in pods) are dry and have physical dormancy ("hardseededness") resulting from densely packed layers of palisade cells impregnated with water-repellent substances which constrains imbibition of water (Baskin et al., 2000; Baskin and Baskin, 2014), a necessary step for germination. Thus, based on studies of other organisms (reviewed in Hämäläinen et al., 2017), we anticipated that gut-passage in the snakes would aid in chemical and mechanical scarification and accelerate germination frequency and rate. In other studies involving reptiles, the effects of gut passage on germination rate and frequency are mixed; in some cases both germination rate and frequency are accelerated (e.g., Yang et al., 2021), yet in others neither of these effects are observed (e.g., Castilla, 2000). Clearly, for reptiles, studies of diploendozoochory are in their infancy and it would be premature to make hard conclusions at this time based on the little available information (Hämäläinen et al., 2017; Reiserer et al., 2018). Nonetheless, the importance of positive effects of gut passage, such as described in other studies (Hämäläinen et al., 2017), cannot be overlooked and should encourage further research in this understudied area of ecology.

We provide several possible explanations for our results with respect to the second hypothesis tested in the primary study. Foothill Palo Verde (*P. microphylla*) is a species in which the seed crop is comprised of both non-dormant and dormant seeds and thus diversified germination behavior is exhibited (Bowers and Turner, 2002; Bowers, 2004). Consequently, a variable proportion (e.g., 20 to 34%) of them can germinate shortly after dispersal from their pods and, importantly, without scarification (Bowers, 2004). The dormant seeds can persist into a second season (or even longer) and require exposure to environmental scarification (high heat, rain, wind, and abrasion) for germination to occur (Bowers and Turner, 2002; Bowers, 2004). Second, in germination studies of *P. microphylla*, we suspect capturing subtle differences in germination rate and frequency will likely require a much larger sample size of seeds to achieve statistical significance for a potentially small effect. Perhaps a 10-fold increase of seeds (e.g., 1000) would be required to overcome the abovementioned problems associated with dormant and non-dormant seed types (see **Figure 5**). Finally, because wet heat appears to be an important release of dormancy in a closely related species of tree from Mexico (*Parkinsonia aculeate*), and thus likely others (Van Klinken et al., 2006), subjecting *P. microphylla* seeds to warmer conditions (e.g., 38–45°C) during germination tests in future studies is warranted.

Similar to the results of the primary study involving Western Diamond-backed Rattlesnakes (*C. atrox*) mice impregnated with seeds of *P. microphylla* were consumed by the Sonoran Gophersnake (*P. catenifer*) and Desert Kingsnake (*L. splendida*). Some of those seeds that transited the digestive tracts retained viability and germinated (see **Supplementary Figure 3**). Nonetheless, when compared to the primary study, germination frequency was significantly greater in the primary study (z-test, two-tailed: $z = 7.140$, $p < 0.001$). This result was likely due to greater trial duration in the primary study (trials were run for 128 days) and germination conditions were likely superior (e.g., less moisture, warmer, and better air circulation) for *P. microphylla*. Mold was commonly associated with seeds kept in their feces in trials 1 and 2 of the secondary study. However, we suspect that the highly moist conditions and lack of air flow in petri dishes contributed to this issue. In the Sonoran Desert, similar condition would rarely be encountered. Clearly, in the secondary study, better results were obtained when seeds were removed from the feces and urates. Germination conditions that more closely mimic natural situations (e.g., drier and warmer) are warranted in future studies, which we envision to include performing tests under a range of natural conditions (e.g., outdoor plots).

We provide herein support for the role of viperid and colubrid snakes as important agents of seed rescue and dispersal in nature, highlight their importance as potential ecosystem engineers, and offer sound justification for future field-based studies (Reiserer et al., 2018). Clearly, more research is needed, especially studies that are field-based, to provide context and to better understand the ecological and evolutionary ramifications of this fascinating, yet mostly understudied, diploendozoochorous system (Franklin et al., 2016). Although our current focus has been on organisms of North American deserts, clearly other regions (e.g., tropics) should be explored (Reiserer et al., 2018; Dugger et al., 2019). Furthermore, other plant and snake species would be desirable to study purely for inclusion of greater biodiversity and exploration of potential variation (Hämäläinen et al., 2017).

CONCLUSION

Topics closely related to seed dispersal and their fates will need to be investigated in field-based studies of diploendozoochory in snakes. For example, despite an abundance of research on defecation sites of lizards, the closest extant relatives of snakes, similar detailed studies are nonexistent, to the best of our knowledge, for wild snakes. Unquestionably, the fate of eliminated seeds in instances of diploendozoochory by snakes and other vertebrates may be further influenced, both positively and negatively, by abiotic (e.g., rain and temperature) and biotic factors (Vander Wall and Longland, 2004). Invertebrates, for instance, such as ants (Pascov et al., 2015; Luna et al., 2018; Anjos et al., 2020) and dung beetles (D'hondt et al., 2007; Midgley et al., 2015), are common vectors in several ecosystems that disperse and alter ground-based seeds both mechanically and chemically (Franklin et al., 2016). Given that only anecdotal data are available, the ecology of defecation sites in snakes and the fate of seeds present in their feces remain open research questions. Indeed, as stated by Anni Hämäläinen and her colleagues (Hämäläinen et al., 2017, p. 13), "It is currently unknown how important the phenomenon (of diploendozoochory) is ecologically, but given its potentially vast prevalence and the possible implications, it is possible that ignoring it could impair the interpretation of broad ecological patterns or hinder conservation efforts." Importantly, it is incumbent upon us to comment that many of the vipers and other snake species that are candidate ecosystem engineers are themselves endangered for various reasons, including from direct persecution by humans (Maritz et al., 2016; Birskis-Barros et al., 2019; Fathinia et al., 2020). It is hoped that highlighting their potential new role as agents of seed rescue and secondary dispersal for deserts and other ecosystems will encourage both academic and public involvement (e.g., citizen scientists) in generating interest and legislature for their protection and long-term conservation.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Dryad Digital Repository: https://doi.org/10.5061/dryad.65gr2.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because our study involved collecting seeds from the fecal wastes of museum and zoo snakes. No animals were harmed in this study. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

GS and RR conceived the study. GS, AS, WH, SB, JH, RZ, and CF collected the data. RR, GS, AS, and MD analyzed data. GS, RR, AS, WH, MD, and HG wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.761293/full#supplementary-material

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