

Research



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Seed ingestion and germination in rattlesnakes: overlooked agents of rescue and secondary dispersal

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Seed dispersal is a key evolutionary process and a central theme in the population ecology of terrestrial plants. The primary producers of most land-based ecosystems are propagated by and maintained through various mechanisms of seed dispersal that involve both abiotic and biotic modes of transportation. By far the most common biotic seed transport mechanism is zoochory, whereby seeds, or fruits containing them, are dispersed through the activities of animals. Rodents are one group of mammals that commonly prey on seeds (granivores) and play a critical, often destructive, role in primary dispersal and the dynamics of plant communities. In North America, geomyid, heteromyid and some sciurid rodents have specialized cheek pouches for transporting seeds from plant source to larder, where they are often eliminated from the pool of plant propagules by consumption. These 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, the role of snakes in seed dispersal remains unexplored. Here, using museum-preserved specimens, we show that in nature three desert-dwelling rattlesnake species consumed heteromyids with seeds in their cheek pouches. By examining the entire gut we discovered, furthermore, that secondarily ingested seeds can germinate in rattlesnake colons. In terms of secondary dispersal, rattlesnakes are best described as diplochorous. Because seed rescue and secondary dispersal in snakes has yet to be investigated, and because numerous other snake species consume granivorous and frugivorous birds and mammals, our observations offer direction for further empirical studies of this unusual but potentially important channel for seed dispersal.

1. Introduction

Seed dispersal has played a foundational role in the population ecology and evolutionary dynamics of terrestrial plants throughout their evolution [1–3]. Dispersal, which can occur by various abiotic and biotic mechanisms, allows propagules to (i) escape competition with conspecifics and relatives, (ii) reach safe locations for germination, and (iii) colonize distant sites (e.g. [4–7]). Quantifying seed dispersal and subsequent success (e.g. germination, colonization), however, is fraught with challenges [3], especially in plants capable of long-distance dispersal [8]. Populations of primary producers in most terrestrial ecosystems are regenerated, maintained and expanded through various mechanisms of seed dispersal. By far the most common biotic seed dispersal process is zoochory, whereby propagules, or fruits containing them, are dispersed by inadvertent ‘hitchhiking’ (e.g. via fur, feathers, airflow of vehicles) or consumed intact by various animal species [9]. Some consumers temporarily store seeds in specialized structures (e.g. cheek pouches, bird crops) before consumption, whereas others fully ingest them while foraging. Stored seeds, whether

damaged or intact, are ultimately passed through the gut and returned to the environment via faeces. When seeds transit the gut intact and emerge viable, this process is termed endozoochory [9,10], a common seed dispersal mechanism documented in most vertebrate groups including fishes [11], amphibians [12,13] and non-avian reptiles: lizards [14,15], turtles [16–18] and crocodylians [19]. In general, endozoochory is primarily studied and best understood in birds [20,21] and mammals [9,10,22–24].

Although many plant species are dependent on invertebrate and vertebrate animals for their pollination, seed germination, and seed dispersal [25,26], seed predation destroys vast numbers of propagules and thus sets up an evolutionary arms race of adaptation and counter-adaptation. Plants with high rates of seed predation have evolved myriad adaptations to minimize seed loss caused by animals [25], e.g. those more-or-less dependent on zoochory often produce seeds with durable integuments, encased in fleshy fruits. This strategy offers protection of seeds from vertebrate predators (primary dispersers) and promotes effective dispersal. Some seeds have vestigial appendages or edible pods that can be consumed without harm to the seed itself [27].

Rodents commonly prey on seeds (granivory), such that globally they play critical roles in primary dispersal and plant community dynamics [28–30]. In particular, heteromyid (e.g. *Chaetodipus*, *Dipodomys* and *Perognathus*) and geomyid (e.g. *Geomys* and *Thomomys*) rodents of North America have cheek pouches for transporting many small seeds from source plants to underground caches ([30–32]; electronic supplementary material, figure S1). While these speciose groups of small, often common, rodents play a role as primary seed dispersers in diverse environments, particularly deserts, their primary relationship to plants is as seed predators. Like many other primary seed dispersers, these rodents are eaten by birds-of-prey (e.g. hawks and owls), canids, mustelids and felids (e.g. [33]). Such predators thus can be secondary dispersers by consuming seed-carrying rodents, a process termed diplochory (secondary seed dispersal) or diploendozoochory [9,10].

In many New World biomes, rattlesnakes (Viperidae: genera *Crotalus* and *Sistrurus*) are common and significant predators on small mammals, including heteromyids and geomyids [34–36]. However, unlike raptors, coyotes, bobcats, and many other endothermic predators of rodents known to be or implicated as secondary seed dispersers, the potential role of these vipers and other snakes as significant seed dispersers remains unrecognized and largely unexplored [37].

Here, using museum-preserved specimens, we show that three species of desert-dwelling rattlesnakes incidentally ingested whole, viable seeds that were in the cheek pouches of their wild heteromyid prey. By examining the entire gut (stomach to colon), we demonstrate that secondarily ingested seeds sometimes germinated in rattlesnake colons. We then explore the potential significance for plants of secondary seed dispersal by rattlesnakes, as well as the possibility that plant dispersal by snakes is a widespread, ecologically significant phenomenon.

2. Material and methods

(a) Specimens

We investigated formalin-preserved, ethanol-stored, wild-collected (Arizona, California) specimens of adult rattlesnakes

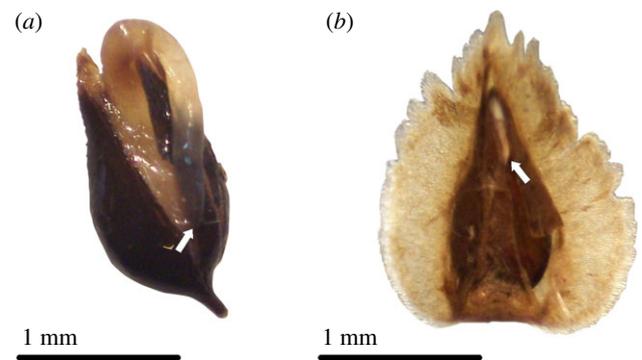


Figure 1. Examples of germinated seeds from the lower intestines of rattlesnakes examined in this study. (a) *Achnatherum hymenoides* (Indian ricegrass). (b) *Cryptantha pterocarya* (wingnut cryptantha). Arrows denote the root radicle tip. See table 1. (Online version in colour.)

curated in the Museum of Vertebrate Zoology, University of California at Berkeley (electronic supplementary material, appendix S1). Gastrointestinal (GI) tracts of 50 individuals were examined: 42 *Crotalus cerastes* (sidewinder), four *C. scutulatus* (Mojave rattlesnake) and four *C. pyrrhus* (southwestern speckled rattlesnake). Three primary GI regions were examined: stomach, small intestine and large intestine including colon.

(b) Analysis

Identification of prey remains and seeds was aided by the use of a Bausch & Lomb 7X-30X dissecting microscope, through which we photographed exemplar seeds. Diets of these species of rattlesnakes have been discussed in detail [38–41]. Where possible prey remains were identified to genus and species; otherwise they were assigned to higher taxonomic categories (e.g. rodent, lizard). Seeds in each gut region were counted and exemplars photographed for identification by T. R. Van Deventer (Arizona-Sonora Desert Museum), based on high-magnification images. Seeds were scored as germinated if a root radicle was clearly visible (figure 1).

3. Results

Among the 50 snakes we examined (table 1), prey were found in 22 stomachs, 17 upper intestines and 25 lower intestines. Rodent remains ($n = 36$) included 17 *Chaetodipus* sp. in 17 (34%) snakes, three *Dipodomys* in three (6%) snakes and one *Neotoma* in one (2%) snake. One each of three lizard species was identified in GI contents of *C. cerastes*, including *Dipsosaurus dorsalis* (desert iguana), *Aspidoscelis tigris* (tiger whiptail) and *Coleonyx variegatus* (western banded gecko). Rodent remains (e.g. hair, teeth) were present in 45 snakes (90%) and lizard remains were present in nine snakes (18%).

A total of 971 seeds were examined in the GI tracts; nearly half (439 seeds) were *Erodium cicutarium* (redstem stork's bill or pinweed) followed by two seed species (204 and 192 seeds) that were distinctive but remained unidentified; these three species made up 86% of the total seeds scored. Three of the four germinated seed species were identified as *Cryptantha pterocarya* (wingnut cryptantha), *Achnatherum hymenoides* (Indian ricegrass) and *Poa* sp. (bluegrass). All germinated seeds ($n = 19$) were confined to the large intestines, and most of them (11, 57.9%) were from the colon of one *C. scutulatus* whose stomach contained rodent remains (*Dipodomys* sp.). The distribution of seeds among the three rattlesnake species examined is shown in table 1. All but

Table 1. List of 14 different seed species ($N = 971$) recovered from the stomachs ($n = 283$) and the intestines ($n = 688$) of museum-preserved rattlesnakes in this study. Of these, six were identified to species and two to genus. A total of 19 seeds were scored as germinated from the lower intestines. An asterisk beside occurrence labels denotes observed germination in: c = *cerastes*, p = *pyrrhus*, s = *scutulatus*. See figure 1.

seed species	frequency/germinated	occurrence	seed description
<i>Erodium cicutarium</i>	439/0	c, p, s	thin, spear-shaped, hairy
?	204/13	c*, p*, s*	kidney-shaped
?	192/0	c, p, s	resembled a sesame seed
<i>Cryptantha barbiger</i>	34/0	c, s	pointed ovate, ventral cleft, small bumps on dome
<i>Poa</i> sp.	30/1	c*	long, slender grass seed
?	27/0	c	kidney-shaped, in pod
<i>Eschscholtzia californica</i>	17/0	c	small (1 mm) peppercorn-like
?	9/0	c	nut-like
<i>Achnatherum hymenoides</i>	6/4	c*	pod-like
<i>Cryptantha</i> sp.	4/0	c	pointed ovate with dome/opposite keel
?	4/0	c	trilobed rose hip-like pod with a smooth pointed seed
<i>Amaranthus albus</i>	3/0	p	spheroid
<i>Cryptantha pterocarya</i>	1/1	s*	pointed ovate with leafy flange
?	1/0	s	short grass seed

one (49, 98%) of the snakes contained at least one seed in their GI tracts (range = 0–175 seeds, mean = 12.6 ± 27.9 s.d.). Of 971 seeds, 283 were in stomachs and 688 in intestines.

For statistical analysis we collapsed data into upper (stomach and small intestine) and lower (large intestine and colon) GI tracts. There was a significant difference in seeds germinated from upper and lower GI tracts (0/283 [0%] versus 19/688 [2.76%], respectively; Z -test, $z = -2.8234$, $p = 0.0048$, two-tailed; $\alpha = 0.05$). We are confident that seeds scored as germinated (figure 1) had initiated root radicle development after ingestion and following transit through the stomach and upper intestine, because no germinated seeds were found in cheek pouches of the rodents examined in snake stomachs, nor in upper parts of snake digestive systems. There was no evidence that whole seeds secondarily ingested by the rattlesnakes examined were damaged or had loss of viability.

4. Discussion

To our knowledge, the only previously published work on seed ingestion and germination in snakes was by T. R. Engel [37], who investigated the fate of diaspores (e.g. seeds, fruits) placed in prey fed to captive black-necked spitting cobra (*Naja nigricollis*, Elapidae), puff adder (*Bitis arietans*, Viperidae), several species of beaked snakes (*Rhamphophis*, Lamprophiidae), and the northern African python (*Python sebae*, Pythonidae). Gut-passage time was 2–14 days, and in several cases defaecated seeds had germinated. Diaspores recovered from faeces were always intact, but there was no evidence that gut-passage improved germination. Here, we have provided compelling evidence from GI contents of museum specimens that free-living individuals of three species of North American vipers, by incidentally consuming seeds transported by their rodent prey, likely promote plant dispersal. Many of the numerous seeds in GI tracts of rattlesnakes appear to remain viable throughout passage, based on their often intact condition and our

discovery of 19 germinated seeds in lower intestines, primarily colons. Because certain rodents (e.g. heteromyids, geomyids) transport seeds in cheek pouches rather than immediately ingesting them, snakes that prey on these rodents are best characterized as agents of secondary seed dispersal (diplochory) rather than being diploendozoochorous [9,10].

To generalize from our findings, four characteristics of many snakes make them potentially important for secondary seed dispersal. First, unlike canids, mustelids and other omnivorous mesopredators that are secondary seed dispersers, all snakes are strict carnivores [42,43]. Consumption of plant materials (e.g. fruits) by snakes is rarely reported and mostly incidental [37,44,45]. Moreover, snakes are not capable of digesting cellulose, hemicellulose, lignin and pectin found in diaspores [43,46]; thus, seed damage due to digestion (e.g. chemical and enzymatic breakdown) is less likely in their GI tracts [37]. Second, snakes are unusual among vertebrates in being gape-limited predators that subjugate and swallow prey whole without mastication [47,48]; hence, mechanical damage to seeds during ingestion is unlikely. Viperids are exceptional in that some consume individual prey items greater than 150% of their mass [47]; consequently, depending on the prey species, a single meal might include many small diaspores. Third, digestion in some snakes is protracted, with long-term faecal retention in the hindgut [49]. Gut passage time (GPT, ingestion to defecation) generally correlates with body shape, such that GPT is longer in stout species (e.g. viperids) than in slender species [49]. For example, in sidewinders (*Crotalus cerastes*), our primary study species, GPT ranges from 11–24 days [50], and is likewise protracted in other desert-dwelling rattlesnakes (e.g. *C. atrox*, *C. scutulatus*; [G.W.S. 2001–2010, personal observation]). Such long GPTs might facilitate both germination and long-distance seed dispersal [51,52]. Because many diaspores are relatively impervious to water and gases, which can prevent or delay germination, specific conditions during digestion (e.g. moisture, temperature and GI

chemicals) might enhance germination by way of scarification. Scarification is the process that alters diaspores to break dormancy [51,52]. Moreover, snake faeces, both in the colon and excreted, might provide especially rich nutritional microenvironments for germinating seeds. Last, behavioural and ecological attributes likely magnify the above morphological and physiological features. Desert-dwelling rattlesnakes and other vipers can be abundant (e.g. western diamond-backed rattlesnake, *Crotalus atrox*, more than 50 adults per km²), an individual is able to consume 12–20 rodent meals and potentially hundreds of seeds [53] during an active season lasting 25–30 weeks, and individuals occupy large home ranges, in which they sometimes travel more than 2 km within a few days [36,54]. Consequently, vast numbers of diaspores may potentially achieve exceptionally long secondary dispersals, perhaps several times greater than those distributed by the rodents themselves [29,55].

We suspect that among the more than 3500 extant snake species described, many consume seed- and or fruit-transporting prey, and thus should be studied and appreciated as seed rescuers and secondary dispersers, perhaps even ecosystem engineers, in addition to their recognized predatory functions. To mention only a few potential examples, in North America, timber rattlesnakes (*Crotalus horridus*) frequently eat chipmunks (*Tamias* sp., Sciuridae; [56]) and non-venomous gopher snakes (*Pituophis catenifer*) often prey upon their name-sake rodents (Geomyidae; [57]). Mammals in those taxa transport seeds in cheek pouches, as do convergent species in other arid regions [58]. Granivorous birds are also taken by snakes, including an extraordinarily specialized Old World viper (*Pseudocerastes urarachnoides*; [59]), and thus those relationships might also include secondary seed dispersal.

Prospects for gaining a broader and richer understanding of seed dispersal by snakes clearly merit further investigation

[60,61]. Crucially, future research should follow T. R. Engel's [37] lead and test for seed viability after passing through GI tracts of diverse snakes, including the possibility that associated faeces are nutritionally important for seedlings. Because many rattlesnakes and numerous other snake species (e.g. boids, elapids and pythonids), are sufficiently large for radio-telemetry (reviewed in [54]), we also envision field-based studies using next-generation molecular methods [62,63] to investigate long-distance transport and fitness of secondarily dispersed seeds. Indeed, rather than categorizing snakes as strictly predators, we should initiate research on their potential roles in ecosystem services [13,21,64], particularly in deserts and tropical biomes, where vipers and other snakes are especially diverse [42,47,65].

Ethics. Our study used museum curated animals preserved prior to this research. No animals were harmed in this study.

Data accessibility. Data are available from the Dryad Digital Repository at: <https://doi.org/10.5061/dryad.65gr2> [66].

Authors' contributions. R.S.R. and H.W.G. conceived the study. R.S.R., G.W.S. and H.W.G. analysed data. G.W.S., R.S.R. and H.W.G. wrote the manuscript.

Competing interests. We declare we have no competing interests.

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