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RESEARCH ARTICLE

Sandy seeds: Armour or invisibility cloak? Mucilage-bound sand physically protects seeds from rodents and invertebrates

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Abstract

1. Seeds represent a stage of a plant's life cycle that is extremely vulnerable to predation, which unlike most vegetative herbivory, is fatal to the individual. As such, understanding the distribution and abundance of plants may rely on understanding seed defences: characteristics that make seeds more difficult for granivores to locate, less beneficial for granivores to consume or both.
2. Seeds that produce mucilage are widespread, found across many families and species. Although short-term (single day) studies indicate that mucilage may be a fundamental seed defence found throughout the plant kingdom, it is not clear to what extent mucilage provides long-term benefits to seeds by reducing granivory. Moreover, it is not clear whether this long-term defence occurs because mucilage reduces seed apparency as substrate-coated seeds are more difficult to detect, whether substrate-coated seeds are less valuable or both.
3. In the first field experiment, we factorially manipulated sand coatings, background sand colour and granivore community using feeding depots to test the mechanistic basis of mucilage-bound sand as a seed defence against diverse granivores. We found that the sand coating significantly extended chances of seeds remaining over the 101-day trial, during which rodents were the primary granivores, and our coloration manipulation suggests that the effect was almost entirely physical. We found that whether a seed's sand coating matched its background did not greatly affect chance of removal, leaving the crypsis mechanism unsupported.
4. We conducted a follow-up field experiment to test the background-matching hypothesis in more detail, using 20 sand colours and two colours of flax seeds. We again found no support for crypsis, corroborating the finding that mucilage-bound sand provides a primarily physical defensive benefit.
5. *Synthesis*. The totality of the results from this and previous studies across granivore taxa and plant species suggests that seed mucilage is a widespread and highly effective physical defence employed by many plants against diverse granivores in many environments

KEYWORDS
crypsis, foraging behaviour, granivory, insects, physical defence, rodents, seed mucilage, seed predation

1 | INTRODUCTION

Granivory may select for seed traits that deter granivores (e.g. thick seed coats, tannins, capsacin). Granivory might also select for traits that reduce apparency, making it difficult for granivores to locate seeds (Brayton & Capon, 1980; Cook, 1972; Cook et al., 1971). Importantly, granivores are a taxonomically disparate guild, and different granivore species differ in nutritional requirements, sensory modalities, physiological requirements and so on (Brown et al., 1979; Crawley, 1989). Because defensive traits may protect seeds against one granivore species or guild but not another, understanding the significance of seed defence requires understanding which granivores are most affected by a particular trait. Here, we use field experiments capable of evaluating different granivore guilds to investigate how a single trait—seed mucilage—affects removal of seeds by multiple granivore guilds.

Seed mucilage consists of a layer of polysaccharides that becomes gelatinous when wetted (Figure 1: top row) and is found broadly across thousands of species of plants (Grubert, 1981). This sticky seed coating has several demonstrated defensive benefits. Once dried, mucilage strands tightly bind the seed to whatever it is in contact with. Often, this is the ground, and this binding makes the seed less likely to be removed by harvester ants (Engelbrecht & García-Fayos, 2012; Gutterman & Shem-Tov, 1997; Pan et al., 2021; Yang et al., 2013). The mechanism behind the defensive value of physical binding to the substrate seems to be simply the force of attachment and thus the difficulty of exploitation, as seeds with greater anchorage strength were removed at lower rates (LoPresti et al., 2023; Pan et al., 2021). In areas with loose substrate, wetted mucilage binds substrate, which remains firmly bound to the seed once dry (Figure 1: top row). This substrate coating effectively protected chia *Salvia columbariae* seeds from both harvester ants and vertebrates (Fuller & Hay, 1983), and protected 48 of 53 tested plant species against harvester ants (LoPresti et al., 2019; Figure 1: middle row left). The substrate coatings could present a physical barrier, leading to a higher exploitation cost (also see marine and

FIGURE 1 Top Row (L-R): Bare, mucilage-imbibed and mucilage-bound seeds of *Linum usitatissimum* (Linaceae), *Physaria ovalifolia* (Brassicaceae), *Salvia hispanica* (Lamiaceae), *Lepidium sativum* (Brassicaceae) and *S. sclarea* (Lamiaceae). Middle Row (L-R): harvester ants, *Pogonomyrmex subdentatus*, struggling with a sandy *L. usitatissimum* seed; our black background choice treatment, our blue background choice treatment. Bottom Row (L-R): an open depot; a rodent-excluded depot.

freshwater examples in Bellwood & Fulton, 2008; Vadeboncoeur & Power, 2017). Substrate coatings could also decrease the apparency of the seed by enhancing crypsis, as a substrate coating will match the surrounding substrate, and seeds may be protected by substrate matching (Brayton & Capon, 1980). These two mechanisms were hypothesized by Fuller and Hay (1983) to explain their results. LoPresti et al. (2019) coated flax seeds with substrate that matched or did not match the background and found no differences in removal rate by harvester ants *Pogomyrmex subdentatus*, suggesting that the benefit was purely physical, not through reduced apparency. Previous studies that have tested a crypsis effect of substrate entrapment on plants and seeds have found no support for crypsis as a mechanism behind the defensive function (LoPresti et al., 2019; LoPresti & Karban, 2016) and further directed tests may shed light on whether those results are generalizable.

While these studies indicate that mucilage may play an important role in reducing granivory by reducing the quality of seeds and increasing handling costs to granivores, two important considerations are that the effectiveness of mucilage via both means (physical protection and crypsis) may depend critically on the granivore guild and the amount of time that seeds are exposed to granivores. For example, ants and rodents are both important granivores in many systems (e.g. Brown et al., 1979; Crawley, 1989; Fuller & Hay, 1983; Orrock et al., 2003) but these guilds differ greatly in seed-handling abilities as well as the primary sensory modalities used to detect seeds. Previous studies, including our own, on the defensive value of mucilage are limited in their applicability because of a restriction of granivores and/or a very short study period. Only ants were considered in Ready and Vinson (1995), Gutterman and Shem-Tov (1997), Engelbrecht and García-Fayos (2012), Yang et al. (2013), LoPresti et al. (2019) and Pan et al. (2021); in fact, the only study not to restrict granivores to ants was Fuller and Hay (1983). Many of these studies also had very short study periods (Fuller & Hay, 1983; Gutterman & Shem-Tov, 1997; LoPresti et al., 2019; Pan et al., 2021; Ready & Vinson, 1995; Yang et al., 2013). While harvester ants are important granivores in many locations worldwide and may consume nearly all favoured seeds in areas where they are common (Silvestre et al., 2019; Tevis, 1958), many other granivores are active in areas where harvester ants occur, and differ in important aspects of their ecology (foraging modalities, caching behaviour, seasonal activity and more). Furthermore, these ants are absent from a great many regions. These studies have provided solid evidence for a short-term benefit of mucilage in reducing granivory from a limited suite of granivores. Yet, these experiments are incapable of determining whether the benefits of mucilage extend to seeds exposed for longer periods that may more closely approximate natural situations, where seeds may be vulnerable to diverse granivores for extended periods before they germinate or escape via entry to the seed bank (Chambers & MacMahon, 1994). Importantly, these previous studies are also incapable of determining whether the defensive role of mucilage is inherently different between granivore guilds. To understand the ecological significance of mucilage, studies are needed that accommodate multiple granivore guilds, realistic deployment durations and are capable of explicitly separating defence vs. crypsis-mediated mucilage effects across granivore guilds.

We used a long-term factorial experiment to evaluate the degree to which flax (Linaceae: *Linum usitatissimum*) seed mucilage provides a means of seed defence via physical means, by increasing crypsis or both. Our experiment included treatments to modify access by particular granivore guilds, allowing us to determine whether the relative value of these possible mechanisms is dependent on the identity of granivores. To more carefully investigate crypsis as a true continuum, we did a second experiment quantitatively manipulating visual contrast between seed colour and background.

2 | MATERIALS AND METHOD

2.1 | Field tests of seed removal via physical defence and crypsis: Choice and no-choice trials

To test the physical and reduced apparency defensive functions of mucilage-bound sand with different granivore communities, we performed a factorial field experiment at the Oklahoma State University Department of Plant Biology, Ecology, and Evolution's McPherson Preserve (36.1002, −97.2065). Located in the crosstimbers ecoregion, the preserve consists of a mosaic of oak forests and tallgrass prairie. We performed the experiment in a narrow stretch of prairie undergoing extensive woody encroachment by red cedar *Juniperus virginiana* and sumacs (*Rhus copallinum* and *R. glabra*). Prescribed burnings are administered on a 5-year basis, most recently in spring 2020. As in LoPresti et al. (2019), we used flax seeds (*Linum usitassimum*, Linaceae; from Premium Gold Flax, Denhoff, North Dakota, USA), which are highly mucilaginous, bind to sand tightly, and are large enough to be easily tracked in the field. A congener, *L. sulcatum*, with similarly sized seeds occurs throughout this prairie; therefore, it is very likely many granivores in the area have encountered *Linum* seeds. Diverse invertebrate granivores are found in the study area, including ants (e.g. *Pogonomyrmex barbatus*), beetles, crickets and grasshoppers, and molluscs. Small mammals, including *Sigmodon hispidus*, *Peromyscus leucopus* and *Reithrodontomys megalotis*, are also common in these habitats.

To monitor seed consumption, we used granivore seed depots modified from the design of Bartel and Orrock (2021); the openings were modified from 2.5 cm×2.5 cm to ~7.5 cm×7.5 cm such that cotton rats *S. hispidus* could access the depots. Our factorial experiment is summarized in Figure 2. This design included a treatment that affected granivore access (open to arthropods and molluscs but not rodents or birds; open to arthropods, molluscs, and rodents, but not birds), a sand-background treatment consisting of two pairs of sand background colours (orange & blue; red & black: Activa Sand, Marshall, Texas, USA), and a seed-coating treatment with three levels (bare seeds, sand-coated seeds matching the background and sand-coated seeds that do not match the background). The seed-coating treatment was applied in two different ways to evaluate how granivore choice might be modified by the presence of other

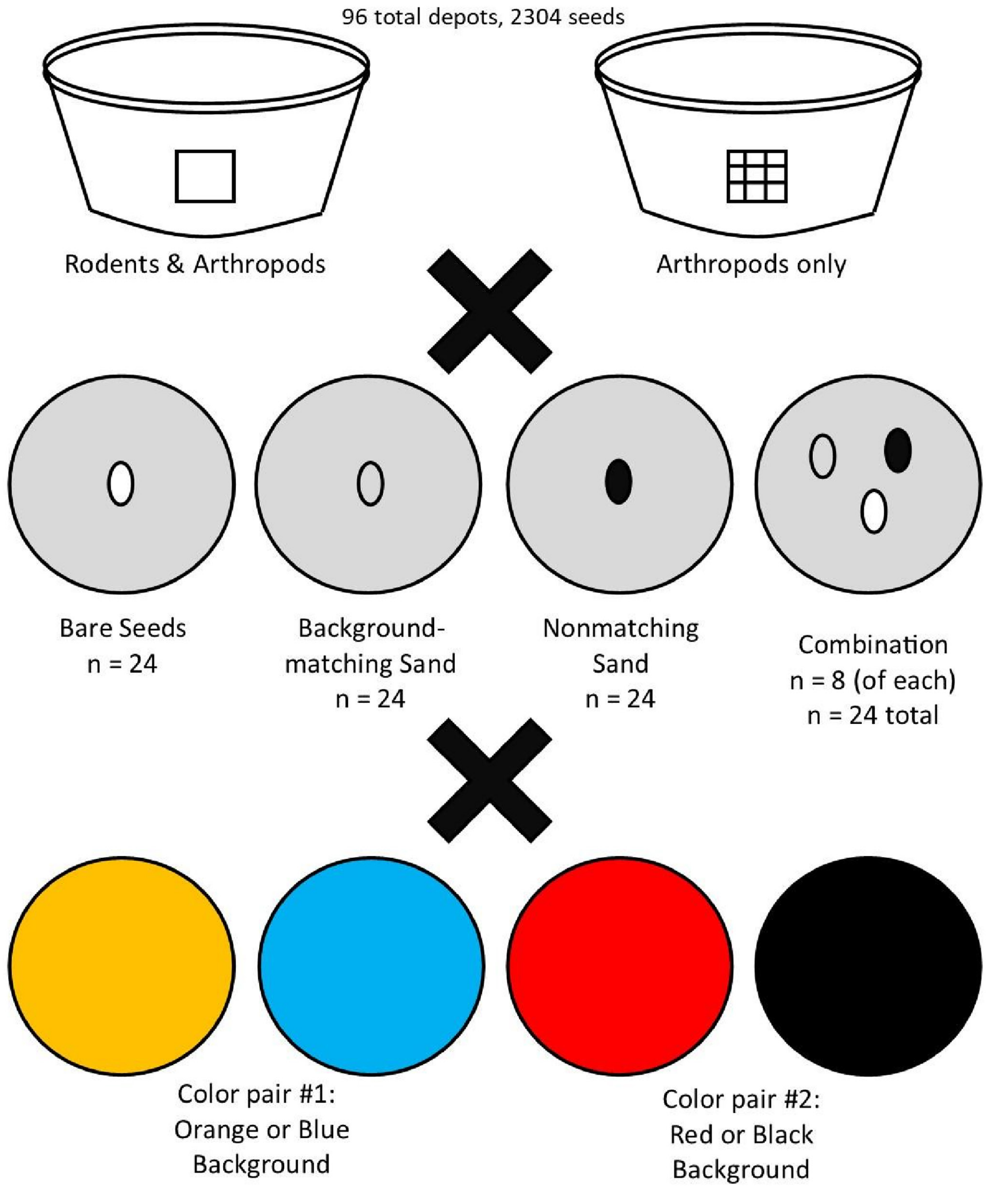

FIGURE 2 The experimental design for the depot experiment in 2021.

seed treatments in the depot: depots were filled entirely with a single treatment (all 24 seeds of the same treatment: 'No-choice') or all three treatments (8 seeds of each treatment 'Choice') in the depot. As in Fuller and Hay (1983) and LoPresti et al. (2019), we coated seeds in sand by covering wetted seeds in sand and allowing them to dry naturally for over 24 h.

The depots were placed in three roughly parallel transects of 32 depots each, with >15 meters between depots. Treatment placement was randomized within each transect. We placed 95 of the 96 depots out on 16 March 2021; however, we ran out of blue sand and were unable to set up the final one until 18 March. On days 7, 14, 28, 42, 78, 91 and 101, we sifted the sand in the depots, counting the remaining seeds. Several depots were flooded during heavy rains; any seeds where the treatment may have been compromised (e.g. if a bare seed became imbibed and became partially coated with background sand) were replaced at this time. We use the number of intact seeds present in the depot as our response variable; many of not most of these seeds were consumed, as we commonly noted seeds destroyed within the depot (e.g. seed fragments).

2.2 | Bare seed contrast experiment

To explicitly test whether visual crypsis was responsible for any of the observed results with the primary granivores in the previous experiment (rodents), we did a follow-up study in February–April 2022. On 14 February 2022, we set up 40 depots with 20 sand colours (2 depots/colour: 19 colours from Activa Sand, and play sand from Lowe's: Appendix 1: Figure S1) and 12 each of dark and light flax seeds (24 seeds/depot). We monitored the experiment and the field site, terminating it and recording seeds remaining on 8 April 2022, as rising spring temperatures were increasing insect activity and we were less sure that any future removals would be from rodents. Two depots were discarded from analyses; one was chewed on by a coyote (or domestic dog), the other was knocked over by an armadillo digging underneath it. Both lost sand and therefore the numbers of remaining seeds were not necessarily indicative of granivory. Due to little removal early on, only seeds remaining to the final check (i.e. 53 days) was analysed as a binomial response variable.

2.3 | Statistical analysis

We modelled the proportion of seeds remaining over the course of the 101-day experiment with generalized linear mixed models (GLMM) using the package GLMMTMB (Brooks et al., 2017). The use of GLMM, as opposed to Cox-proportional hazard models or accelerated failure time models, allowed us to focus on the odds of seed removal over time, which we believe is more relevant to the perspective of the mother plant, though results remained qualitatively the same regardless of model choice (Appendix 1: Part 2). Seed removal in the choice and no-choice experiments were analysed separately as the experimental setup and data structure were different. We used the binomial distribution as the conditional distribution for models of the choice experiment but used the beta-binomial distribution for models of the no-choice experiment due to overdispersion. We also tried analysing logit-transformed proportion survival with a gaussian conditional distribution as a robustness check; the results remain qualitatively the same.

To quantify the rates of seed removal, we fitted the number of seeds that remained for each observation day (excluding day zero) against the day of the experiment (choice: $n = 489$ treatment group bucket-day observations; no choice: $n = 492$ treatment group bucket-day observations). The rate of seed decline was allowed to vary between groups with different colours of background sand. In the case of models of the choice experiment, the rate of seed decline was further allowed to vary between individual buckets nested in colours of background sand. We included an auto-regressive term of lag one for each unit of replication, as the number of seeds that remaining in each observation day was inherently dependent on the number of seeds that remained in the previous observation.

To compare difference in removal over time among treatment groups, we included rodent exclusion treatment, seed coating treatment and the interaction between exclusion and seed coating as fixed effects nested within day of experiment (i.e. as interactions without main effects) in a set of models. We used an analysis of deviance (Wald χ^2 test) to evaluate the significance of predictors. Unsupported interactions between treatment variables were dropped. We performed post-hoc Tukey contrasts between the factor levels of seed coating treatment using the package EMMEANS (Lenth, 2016).

We performed an analysis of visual contrast for both experiments, using models of granivore vision and colour spectra for each sand colour and the seed colour to generate colour distance between each seed/sand pair (quantification methods in the Appendix 1: Part 1). To more mechanistically quantify the effect of visual contrast on seed removal, we replaced the seed coating treatment variable with the presence/absence of sand coating, taxon-specific colour distance between seed and background, and the interaction between the two, while retaining otherwise the same previous model specification. For the visual contrast experiment, we simply compared colour distance between each seed/sand pair and used it as a predictor in the model. For these analyses, we log-transformed the colour distance in correspondence to Fechner's law (Figure 3). For the first set of experiments (i.e. Figure 2), with many granivores, we fit a model for each taxon-specific colour distance and the best model was selected according to Akaike information criterion (AIC). We repeated this only for rodents in 2022, given the winter season and inactivity of insects. We performed all statistical analysis in R, version 4.05 (R Core Team, 2020). For the 2021 experiment, the colour analysis was added after the experiment was run. Because the experimental design was not made to test quantitative measures of crypsis, we consider these analyses speculative (see Appendix 1: Part 1). The follow-up visual-contrast experiment was designed explicitly for this purpose and targeted only the most important granivore in the

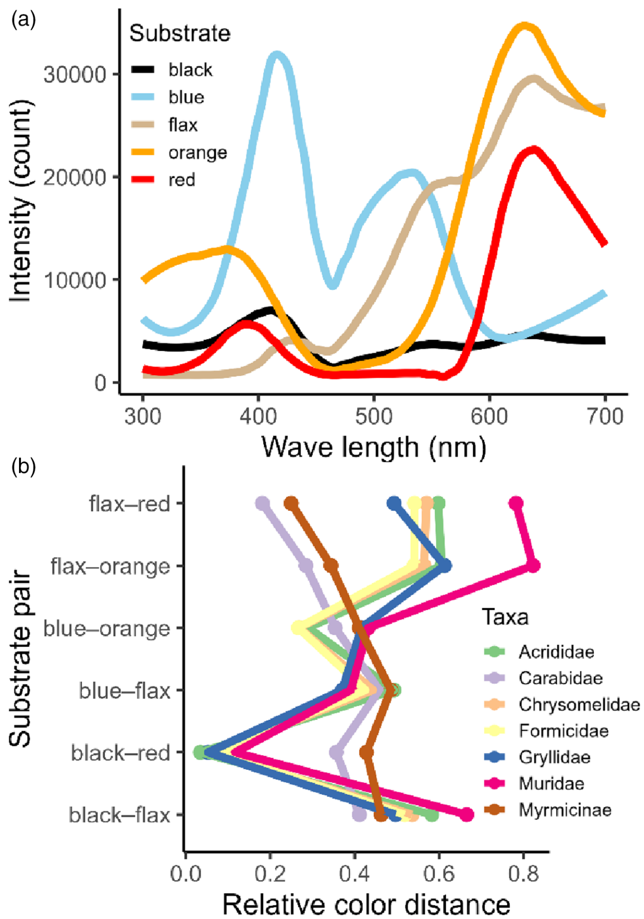

FIGURE 3 Colour difference of substrates used in the main experiment. Panel (a) shows the smoothed spectra of substrates. Panel (b) shows the Euclidean distance between pairwise substrate spectra after they have been projected onto taxa-specific colorspace.

previous study. We used this targeted bare-seed approach because the large number of possible substrate/seed combinations with a substrate coating (over 180) was logistically prohibitive.

3 | RESULTS

3.1 | Overall results

In both choice and no-choice depots, a sand-coating protected seeds from rodent and invertebrate granivores, but not via crypsis (Figure 4). In this system, rodents removed far more seeds than invertebrates. Despite a benefit of a sand coating, the majority of seeds in both choice and no-choice depots were consumed over the course of the 101-day field trial. In both the choice and no-choice analyses, we found strong evidence that rodent exclusion and seed coating treatment affected rate of seed removal (choice: *Pseudo McFadden* $R^2 = 0.32$; no-choice: $R^2 = 0.20$). In no experiment, with any granivore community, did we find strong evidence of any visual crypsis acting, either on sand-covered seeds or with bare seed comparisons to background.

3.2 | Rodent accessible depots had more granivory

In both experiments, rodents accounted for a greater amount of mortality than invertebrates. The corrected mortality rate (Abbott, 1925) for rodents was 94% (in the choice experiment) and 83% (in no choice), compared to 16% (choice) and 58% (no choice) for invertebrates, in the choice and no choice experiments, respectively. In the choice experiment, the odds of seeds remaining in the rodent excluded group declined by 9.4% a day (95% confidence interval (CI) = [6.9%, 12%]) compared to the 13% decline a day in the rodent accessible group (95% CI = [16%, 11%]). The difference was

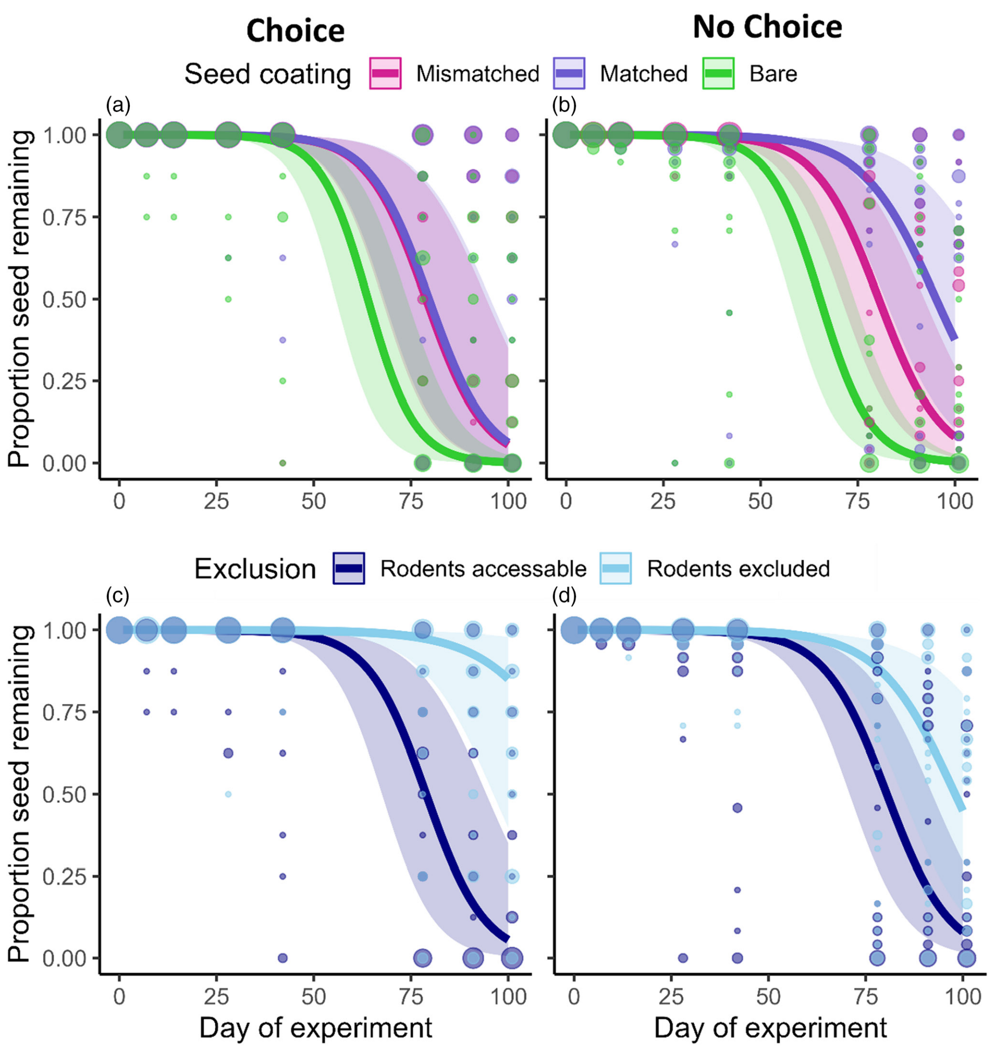

FIGURE 4 Seed survival over the course of the 101-day experiment was strongly affected by rodent exclusion treatment and seed coating treatment. Lines show predicted group means. Ribbons show 95% confidence intervals. Points show the raw data with the size scaled by the number of data points that show the same values. Panels (a and b) show that bare seeds were lost much faster than sand covered seeds in the choice and no-choice experiments, respectively. Panels (c and d) show that rodent exclusion reduced seed predation in the choice and no-choice experiments, respectively.

significant ($\chi^2(1) = 10.0$, $p = 0.0016$) and did not depend on the seed coating treatment (i.e. home colour sand, away colour sand, no sand [bare]: $\chi^2(2) = 1.2$, $p = 0.54$). Results remained largely similar in the no-choice experiment. Odds of seeds remaining in rodent-excluded depots declined by 10% a day (95% CI = [8.6%, 11%]). This decline in odds of seeds remaining over time was 2.3% lower than the 12% decline a day in rodent-accessible depots (95% CI = [11%, 13%]). The difference in survival between the rodent-excluded and rodent-accessible depots was significant ($\chi^2(1) = 7.4$, $p = 0.0064$) and did not depend on seed coating treatment ($\chi^2(2) = 1.0$, $p = 0.60$).

3.3 | Mucilage-bound sand protected seeds from granivory, but not via crypsis

Sand-coated seeds were removed at lower rates than bare seeds, regardless of granivore community or other seed treatments present (i.e. choice/no-choice depots). Seed coating treatment × day explained removal well in the choice depots ($\chi^2(2) = 6.4$, $p = 0.041$). Odds of remaining declined by 10% per day in the colour matched group (95% CI = [8.1%, 13%]), 11% per day in the colour mis-matched group (95% CI = [8.2%, 13%]) and 13% per day in the bare seed group (95% CI = [11%, 16%]). Post-hoc contrast found that both sand-coated treatments have a significantly lower rate of decline compared to the bare seed treatment (colour matched treatment: 3.3% lower, $t = 4.0$, $df = 480$, $p = 0.0002$; colour mis-matched treatment: 3.2% lower, $t = 3.9$, $df = 480$, $p = 0.0003$). However, colour matched treatment did not have a significantly lower decline in remaining in depots as we hypothesized would result from crypsis (0.12% lower, $t = 0.15$, $df = 480$, $p = 0.99$).

We found similar results in the no-choice depots. Seed coating treatment had a significant interaction with day ($\chi^2(2) = 22$, $p < 0.0001$). Odds of remaining in depots declined by 9.0% per day in the colour matched group (95% CI = [7.4%, 11%]), 11% per day in the colour mis-matched group (95% CI = [9.1%, 12%]) and 13% per day in the bare seed group (95% CI = [12%, 15%]). Post-hoc contrasts demonstrated that both sand-coated treatments had a significantly lower rate of decline compared to the bare seed treatment (colour matched treatment: 4.9% lower, $t = 4.7$, $df = 483$, $p < 0.0001$; colour mis-matched treatment: 2.9% lower, $t = 2.9$, $df = 483$, $p = 0.013$). The difference between the colour matched treatment and colour mismatched treatment was slightly greater, in the hypothesized direction of a crypsis effect, but remained not significant (1.9% lower, $t = 1.9$, $df = 483$, $p = 0.13$).

3.4 | Bare seed contrast experiment: No evidence for crypsis

We found no support for the hypothesis that seeds with greater visual contrast with the background would be consumed at higher rates (Figure S2). A binomial mixed model for seed removal including relative contrast did not fit significantly better than one without. In fact, a null model with only the random effect of depot fit better than models with seed colour and log-contrast either together or independently (Appendix 1: Table S2).

4 | DISCUSSION

Seed predation may affect the persistence and distribution of plant populations, the structure of plant communities, and the potential for persistence under global change (Crawley, 2000; Kolb et al., 2007; Tevis, 1958). Our experiment demonstrates that mucilage may provide significant benefits to a seed by reducing removal and decreased seed removal in the presence of both arthropods and rodents. Indeed, the benefits of mucilage may last for a considerable time, providing protection from granivores for the variable, often protracted, period when seeds are at risk (Chambers & MacMahon, 1994). In demonstrating that these long-lasting benefits may protect seeds on the soil surface from a diverse array of granivore guilds, our work helps explain the repeated observation that mucilaginous seeds are found in a variety of different taxa and ecosystems. These results point to a broader defence strategy many plants adopt, where physical protection, an important trait that predicts herbivory (Carmona et al., 2011) and granivory (Lovas-Kiss et al., 2020) is acquired through the entrapment of sand on vegetative or seed surfaces (Lopresti et al., 2018; LoPresti & Karban, 2016). Finally, our results underscore the importance of seed mucilage as a trait that could explain a species' ability to persist and expand in future settings where seed predation may be a limiting factor in establishment.

A mucilage-bound sand coating greatly reduced the chance of removal in both rodent-accessible and rodent-excluded treatments. The effect of the sand coating presence itself drove that reduction; we did not find evidence for crypsis in seeds coated with substrate-matching sand coatings, nor did we find a crypsis effect of bare seeds with rodent granivores. In the previous experiment, we found the same effect of a physical barrier, but not crypsis, using a single granivorous harvester ant species (*Pogonomyrmex subdentatus*) and flax seeds in a series of 2-h trials (LoPresti et al., 2019). Similarly, Fuller and Hay (1983) used 1-, 5- and 8-hour trials to determine that sand coatings protected mucilaginous seeds against harvester ants *Veromesser pergandei* and vertebrate predators (rodents or birds). While the time between dehiscence/dispersal and germination for a seed surely varies greatly, we believe our 101-day trial is far more ecologically appropriate. The strong confirmation of these previous results over longer time periods, in a different region, is reassuring for the generality of these previous findings. Our results add to a very small literature on what is likely a very common and important seed defence of thousands of plant species with mucilaginous seeds (Grubert, 1974, 1981).

Whole plants also become covered in substrate when growing in areas with open, loose substrates, a phenomenon long hypothesized as a potential defence against herbivores (Beal, 1878; Farmer, 2014; Fuller & Hay, 1983; Jürgens, 1996; Lev-Yadun, 2007; an analogous situation occurs with substrate entrapment in algae: Bellwood & Fulton, 2008; Vadeboncoeur & Power, 2017). Glandular-sticky plants and mucilaginous seeds occur in thousands of plant species worldwide (Grubert, 1981; LoPresti et al., 2015; LoPresti & Karban, 2016), yet investigations of a functional role of this substrate entrapment on either seeds or aerial parts are limited to four previous studies (Fuller & Hay, 1983, LoPresti & Karban, 2016; LoPresti et al., 2018, 2019), all of which occurred in xeric or Mediterranean environments. Each of these investigations have demonstrated a clear defensive benefit of substrate entrapment, and those that tested defence mechanism (LoPresti & Karban, 2016; LoPresti et al., 2019, this study) have surprisingly found no support for crypsis. It is worth noting, however, that the relevant herbivores in each of those studies are not particularly visually oriented.

If crypsis was not the defensive function of sand, how exactly does a sand layer physically protect a seed resting on the soil surface? We believe there are four mechanisms potentially operating, the contributions of each being dependent on the granivore taxa in question. The first imposes a physical limitation. (1) There may be some granivores, probably mostly insects, that simply cannot exploit a sand-covered seed, due to the increased mass (up to by 100×: LoPresti et al., 2019), increased volume or inability to remove the sand with their mouthparts or appendages. The next three alter the value of the seed, such that exploitation is not desirable. (2) A sand coating increases handling costs. A flax seed could be carried off directly by a harvester ant, but it often took ants over 10 min to remove enough sand to make the seed carriable to their nest (LoPresti et al., 2019). By increasing the seed volume substantially, rodents which carry seeds to caches in their cheek pouches would be able to carry fewer (notably cheek pouches are usually filled to ~93% of capacity: Vander Wall et al., 1997). (3) Sand may reduce the perception of quality, by not allowing direct assessment of the seed size, identity or condition, leading to underestimation of the benefit or overestimation of the cost (at an extreme, this could lead to perception of the sand-covered seed as something else entirely, a phenomenon known as masquerade; Skelhorn et al., 2010). (4) Sand may be deleterious to ingest to all granivores. Caterpillars which fed on sandy foliage grew more slowly and pupated at smaller sizes, probably due to the extensive mandibular wear that feeding on this abrasive food source caused (LoPresti et al., 2017). External abrasives on plants, that is, dust or entrapped substrate, probably factor into the evolution of high-crowned teeth, allowing extensive wear, in ungulates (Janis & Fortelius, 1988; Kaiser et al., 2013); interestingly, some evidence suggests substrate preference drives tooth height in rodents as well (Williams & Kay, 2001). Our results are consistent with any or all of these mechanistic hypotheses; mucilage-bound sand makes exploitation more difficult and decreases the value of these seeds to both rodents and invertebrates.

Unexpectedly, we found extremely similar results in the choice experiment (bare, matching and non-matching seeds in a single depot) as in the no-choice experiment (independent depots for each treatment). We expected that in the choice depots, there would have been a larger effect, given that the relative perception of quality may be higher for bare seeds when compared to those covered in sand. Second, in the no-choice experiments, encounters with bare seeds could lead foragers to investigate the sand-covered seeds more closely. Yet, our results of similar risk to seeds in each group across the two experiments (i.e. similar removal rates of bare seeds, and a similar benefit for sand coating) surprisingly suggests that the 'neighbourhood' of seeds does not noticeably affect risk to other seeds in the area (see also Veech, 2001). This result is in contrast to others where seed neighbourhood matters greatly (rodents: Ostoja et al., 2013, ants: Tevis, 1958); we do not have a strong explanation for why we did not find these associational effects.

4.1 | Granivore identity and seed defence

By experimentally manipulating access to seeds (Figure 1), our work is capable of evaluating the loss of seeds to invertebrate seed predators relative to the loss of seeds when invertebrates and rodents both have access. Our findings strongly support the importance of rodent granivores in old-field/prairie habitats (e.g. Crawley, 1989; Hulme, 1996; Maron & Simms, 2001; Orrock et al., 2003). It bears mention rodents widely cache many of their collected seeds and that removal by rodents is not certain mortality for the seed (Vander Wall, 1994), while it probably is for the deeply buried seeds collected by harvester ants (Tevis, 1958, but see Dean & Yeaton, 1992). Although rodents were the primary agents of removal, invertebrates nonetheless removed a many of these surface-borne seeds, and both granivore guilds were less likely to consume sand-coated seeds. Our evidence is unequivocal that rodents were the most important granivores in the study, and while sand entrapment was still effective against rodent granivores, it was similarly effective against rodents compared to invertebrates, in contrast to the result found for chia, *Salvia columbariae*, by Fuller and Hay (1983), where mucilage was more effective against vertebrates. In contrast to their design, our study design did not permit access to seed depots by birds. Seeds that better match the background survived better in the presence of doves and quail (Brayton & Capon, 1980; also see Cook, 1972; Cook et al., 1971). However, a clay coating on rice seeds—aimed to reduce predation on crops—deterred bird granivory primarily by serving as a barrier and increasing handling time, not by increasing crypsis (Daneke & Decker, 1988); therefore, it is possible that mucilage-bound sand might serve multiple defensive functions against birds. It is also possible that a sand coating would not deter granivorous birds, assuming they could recognize the seeds, since many keep grit in their crops anyway. Birds are important granivores in many environments (Crawley, 1989; Fuller & Hay, 1983); therefore, the effect of mucilage-bound substrate on their granivory, and the relative contributions of crypsis and a physical barrier deserves attention.

Lastly, it is important to note that species vary in the composition and quantity of mucilage (Grubert, 1974, 1981), and the amount of substrate they entrap (LoPresti et al., 2019). In our previous work, we found a significant, but not strong, correlation across 53 plant species between the mass of sand entrapped and the defensive benefit against harvester ants (LoPresti et al., 2019). Harvester ants exploit sand-covered seeds by peeling off the coating, a time-intensive process, and therefore, the relationship we found would be expected given the increased cost of exploiting seeds with more sand. However, the effect of varying levels of entrapment (including intra-specific variation) has not otherwise been studied and probably differentially affects granivore taxa, and may influence visual or chemical crypsis, as well.

4.2 | Visual contrast to granivores

The matching and non-matching design of the sand coatings in the 2021 experiment was intended to test crypsis in a meaningful, categorical way (crypsis, no crypsis), as has been done in previous studies (LoPresti et al., 2019; LoPresti & Karban, 2016). However, crypsis is more realistically a continuous trait—camouflage does not need to be perfect to be effective. Therefore, as detailed in the supplement, we took colour data for the seeds and sand colours and applied visual models for granivore taxa to get at exact contrasts. This analysis did not produce any substantial additional insights. In the choice experiment, the term for contrast against the background (in the best-fitting model, based on a rodent visual system) did not explain the rate of seed removal. In the choice experiment, there was a very weak effect in the hypothesized direction found in the best-fitting model (for a beetle visual system); however, its effect size was very small. Therefore, we felt that the follow-up 2022 visual contrast experiment was necessary, where we tested 40 contrasts of seed colour and background sand colour in depots that realistically had only rodent granivory in late winter/early spring. Supporting our first finding, we again found no effect of crypsis on these bare seeds, reinforcing that seed crypsis is unimportant against rodent granivory. Nonetheless, we felt that these results backed up the important findings of the rest of the study—that a sand coating itself was a physical barrier—and further studies using visual spectra could lead to a mechanistic examination of seed crypsis with visual granivores (likely important for birds).

4.3 | Mucilage, seed defence and plant life history

Plants growing in unstable substrates—where their seeds are likely to be coated in that substrate (ala this experiment & Fuller & Hay, 1983) and easily buried—are often ruderal species adapted to unstable terrain. Ruderal plant species, across many families, commonly have mucilaginous seeds (Grubert, 1974; Pan et al., 2021, 2022; Ryding, 2001), including many cosmopolitan weed genera (Grubert, 1981; LoPresti et al., 2019). In addition to other functions of mucilage, including seed anchorage in erosive environments (Engelbrecht & García-Fayos, 2012; Pan et al., 2022), the protection afforded to seeds via a sand coating demonstrated here and Fuller and Hay (1983) and LoPresti et al. (2019) may be an important component of this niche, providing a generalized seed defence that is useful against diverse granivores. Of note is that many of these species are common, widespread, successful invasives (i.e. *Capsella bursa-pastoris*, *Lepidium latifolium*, *Euphorbia maculata*, *Prunella vulgaris*, *Arabidopsis thaliana*, *Plantago ovata*, *lanceolata*, *& major* and *Thlaspi arvensis*). Whether mucilage increases survival of these species in their invasive range, against native granivores, deserves careful study.

4.4 | Future directions and potential applications

In finding that mucilage physically protects seeds from granivores, and that this protection does not arise via visual crypsis, our work also sets the stage for future studies to further understand the ecological value of seed mucilage. For example, while our work shows that mucilage provides physical protection for seeds on top of the soil, mucilage may also have affect the fates of seeds once they are buried by physical or abiotic processes. For example, rodent granivores often exhume cached seeds (Smith & Reichman, 1984), and location of buried seeds is facilitated by volatile compounds produced by buried seeds, especially when wet (e.g. Vander Wall, 1998). One unexplored function of mucilage might be to reduce or otherwise modify volatiles emitted from seeds, reducing detection by rodents. Seeds are also often destroyed by microbial seed pathogens; the role of mucilage in affecting seed pathogens remains totally unexplored (it is utilized as a food source by soil micro-organisms: Burrows, 1996; Buse & Filser, 2014). In addition to studies that explore these novel hypotheses, our work suggests that mucilage could be incorporated into conservation and restoration strategies that rely upon seed additions to promote biodiversity (e.g. Orrock et al., in press). In our study, we easily coated thousands of seeds with sand, and these seeds were much less likely to be consumed by granivores. Wetting and coating seeds prior to sowing could provide means to increase the success of plant conservation and restoration in diverse terrestrial systems (see also Daneke & Decker, 1988). This technique could also be implemented for plant species without mucilaginous seeds because seed mucilage is readily obtained and inexpensive (e.g. mucilage is commercially harvested to produce a human dietary supplements, such as Metamucil©). While seed coatings that are thought to reduce plant losses are common in agriculture (e.g. use of neonicotinoid seed coatings), these seed coatings may have highly undesirable effects (Tooker et al., 2017). Much as coating seeds with capsaicin may provide a means to increase restoration success (Pearson et al., 2019), our findings suggest that using existing or added mucilage to coat seeds with sand (or as an adhesive for other coatings) could provide a cost-effective, organic and chemical-free means to reduce granivory in restoration and agriculture.

AUTHOR CONTRIBUTIONS

Eric F. LoPresti, Vincent S. Pan and John L. Orrock conceived and designed the initial experiment; Eric F. LoPresti, Vincent S. Pan and Cecilia Girvin set-up and ran the initial experiment. Eric F. LoPresti, Gabhriel Barber and Sierra Jaeger designed and ran the bare seed contrast experiment. Vincent S. Pan and Gabhriel Barber took the spectrometer measurements of sand and seeds. Vincent S. Pan analysed the data. All authors wrote/edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

None of the authors have conflicts of interest involving ants, seed mucilage or rodents.

DATA AVAILABILITY STATEMENT

All data and code are available on Dryad at: https://doi.org/10.25338/B87647 (Pan, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. AIC of fitted models with different taxon-specific visual model. The interaction between rodent exclusion and log colour distance (nested within day of experiment) was retained in the choice models but dropped in the no-choice models.

Table S2. Model Comparison of the rodent vision models for the visual contrast experiment.

Figure S1. Sand colours used in the continuous visual contrast experiment. Colour names are from the sand producer, ACTÍVA Products, except play sand, from Lowe's Home Improvement. Photos: GB.

Figure S2. Seeds remaining through the entirety of the visual contrast experiment for tan and brown flax seeds. There was no effect of relative visual contrast (log-transformed) or of seed colour (golden flax—pale circles, brown flax—darker triangles) on removal rates. Removal rates overall were far lower in this experiment than in the previous year's experiment—yet there was granivory and rodent faeces in the depots, so we have confidence that these results are robust and accurate. We believe this decrease in removal is due to high acorn production in the dominant oaks (*Quercus marylandica* & *Q. stellata*) in fall 2020 probably contributing to high rodent populations the following spring. Acorn production was low in fall 2021 and therefore, the overall rodent populations were probably low in 2022 while the visual contrast experiment was occurring.

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