RESEARCH PAPER

Built to last a day: The function and benefits of spider mound nests

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Abstract

Nests are crucial to the survival of offspring and reproductive success of the animals that build them. These benefits are subject to change over time due to fluctuating conditions inside and outside of nests. For many species, nests are assumed to benefit offspring until they disperse and therefore, nest destruction prior to offspring dispersal results in reduced reproductive success for parents. However, the consequences of nest destruction to reproductive success, or lack thereof, remain largely unstudied across diverse taxa. Here, we experimentally investigate the function and benefits of nests of a mound-building spider. Mason spiders (*Castianeira* sp.) are wandering spiders that build intricate nests (mounds) on top of their egg sacs. Their offspring inhabit egg sacs at nest sites for up to 7 months, including through winter. We find that despite requiring hundreds of collecting trips and many hours to construct, mason spider nests remain for a small portion of time that offspring occupy nest sites. Our study finds that nest benefits change over time, likely explaining this dynamic. Nests greatly reduce the rate of predation and parasitism of egg sacs by 19.1% and offspring mortality within egg sacs due to abiotic factors by 19.9%. These effects are only present the few days following nest construction. Our study illuminates the idea that nest destruction does not always result in reduced reproductive success for nest builders. We suggest that nest durability, the ability of a nest to withstand environmental conditions, may be subject to natural selection and a critical, yet understudied, aspect of parental care.

KEYWORDS

animal architecture, Corinnidae, Mason spiders, nest building, nest integrity, parental care

1 | INTRODUCTION

For many animals, early life stages are at higher risk of mortality from sources like predation, disease, and environmental fluctuations than other life stages (Clutton-Brock, 2001). To increase their reproductive success, some parents invest time and energy into protecting offspring by building protective structures. Benefits of protective structures like nests have been found across species. For example,

nests increase reproductive success for many mammals (Reichman & Smith, 1990), birds (Mainwaring et al., 2014), reptiles (Angilletta et al., 2009), fish (Ishimatsu et al., 2007; Takegaki & Nakazono, 2000), and arthropods (Hieber, 1992b; Wyatt, 1986). However, the benefits of nests are unlikely to be static through time. From the day they are constructed, conditions outside of nest like environmental conditions and predator dynamics are constantly fluctuating and threatening to damage the nest and/or harm offspring.

The dynamic nature of nest benefits through time has great implications for how much parents invest in building and/or

maintaining nests. Across species, this varies greatly. For example, some nests are actively maintained for years like those belonging to social animals that use nests for generations, including some termite mounds that are occupied for centuries (Erens et al., 2015). In contrast, many songbirds build nests are made to last one breeding season (Mainwaring et al., 2014), and still others, like some amphibians (Giaretta & Menin, 2004) and army ants (Schneirla et al., 1954), construct nests that only need to remain intact for hours to days.

Outside nests, the intensity, frequency, and predictability of environmental conditions may impact the length of time that nests benefit offspring. For example, rainfall has been implicated in nest destruction of vertebrate and invertebrate nests, sometimes zeroing the benefits of nests and leading to their abandonment by parents (Rojas et al., 2019; Thompson & Furness, 1991). In other well-known cases, the presence of predators induces accelerated hatching or fledging of offspring. In these situations, the benefits of nests for aggregated, stationary life stages rapidly decrease as the risk of predation increases (Martin et al., 2018; Warkentin, 1995).

Inside nests, life history traits of species, like how much parental care early life stages require and the length of time that care is necessary, impact the rate that nest benefits decrease over time. For example, scientists have long recognized that the young of most species can be placed along an altricial to precocial spectrum (Augustine et al., 2019). Nests of altricial animals (species where young are born at earlier stages of development) need to stay in nests longer and the benefits of nests decay slowly, whereas many precocial animals do not need nests at all (Starck & Ricklefs, 1998). Over time and as offspring develop, the benefits of nests decrease until they are no longer necessary.

For most species, the length of time that nests benefit offspring and the amount of time that offspring occupy nest sites are assumed to be inextricably linked. In fact, examples of nest destruction prior to offspring dispersal are almost always reported to result in reduced reproductive success for nest builders (Rojas et al., 2019; Thompson & Furness, 1991). However, the consequences of nest destruction to reproductive success, or lack thereof, remains largely unstudied across diverse taxa. We investigate the consequences of nest destruction on reproductive success by untangling the length of time that offspring occupy nest sites, the benefits of nest presence, and how those benefits change over time.

Our study focuses on the mason spider *Castianeira* sp., wandering spiders of the northern Rocky Mountains, USA, that cover their eggs with elaborate mound nests. While most spiders protect their eggs and young with protective structures that minimally involve investment in silk for egg sacs or webs (Hieber, 1992a, 1992b; Toyama, 1999), mason spiders construct mounds made of hundreds of pebbles, leaves, and sticks, held together with silk. Our preliminary observations indicated that despite a large investment in parental care and the fact that offspring persisted at nest sites for many months, mason spider mounds are regularly destroyed. Why do mason spiders go through such effort to build a nest that only remains intact for a small portion of the time that offspring inhabit nest sites? We sought to answer this question by describing the details of parental care and life history of a mound-building spider for the first time. We then experimentally investigated the function of mason spider mounds and how the benefits of mounds change over time. Finally, we discuss why nest duration is an important, yet understudied aspect of parental care.

2 | METHODS

2.1 | Study site and data collection

The mason spider studied here is an undescribed species in the *descripta* group of the genus *Castianeira* (Corinnidae) (Reiskind, 1969). The necessary taxonomic work for species determination of mason spiders is outside the scope of this study. Mason spider specimens have been deposited in UC Berkeley's Essig Museum (EMEC 1,199,520–EMEC 1,199,527).

We studied mason spiders along the Snake River in Bridger-Teton National Forest, WY, USA (43°18'10.3"N 110°46'27.6"W; altitude 1,800 m) in open habitats dominated by sage, alfalfa, and various grasses. These habitats have gravel soil with large rocks scattered throughout. Mason spiders lay egg sacs in the crevices of rocks and build their mounds on top (see Figure 1a,b; *Behavioral description*). We observed 1,368 mounds and filmed the construction of 14 mounds using GoPro (HERO 4) cameras across 4 mound-building seasons (June – September 2015–2018 and in the winter of 2017/18). Each day, we deployed 3–4 GoPro cameras that were mounted on tripods and positioned one meter from egg sacs so as not to disrupt mason spiders during mound construction. We describe mason spider mound-building behavior using observational data collected at field sites in combination with videos of mound construction. We analyzed the videos of mound construction using BORIS (Behavioral Observation Research Interactive Software) (Friard & Gamba, 2016) and ImageJ (MtrackJ) software (Schneider et al., 2012) to collect data on the number of collecting trips per hour and length of collecting trips.

2.2 | Mound removal experiment

We experimentally tested the impact of mason spider mounds on offspring survival over time. In 2017, we identified 188 egg sacs under construction and randomly assigned them to one of four treatment groups. For each treatment, we removed mounds (a) immediately following their completion ($N = 50$), (b) 24 hr post-construction ($N = 51$), and (c) 10 days post-construction ($N = 42$). Control mounds (d) were never removed ($N = 45$). All egg sacs remained in place until they were collected (see below). Mound construction was determined to be completed when mason spiders did not return to the mound for 1 hr. We put a small dab of super glue on top of all mounds to ensure that they remained in place for
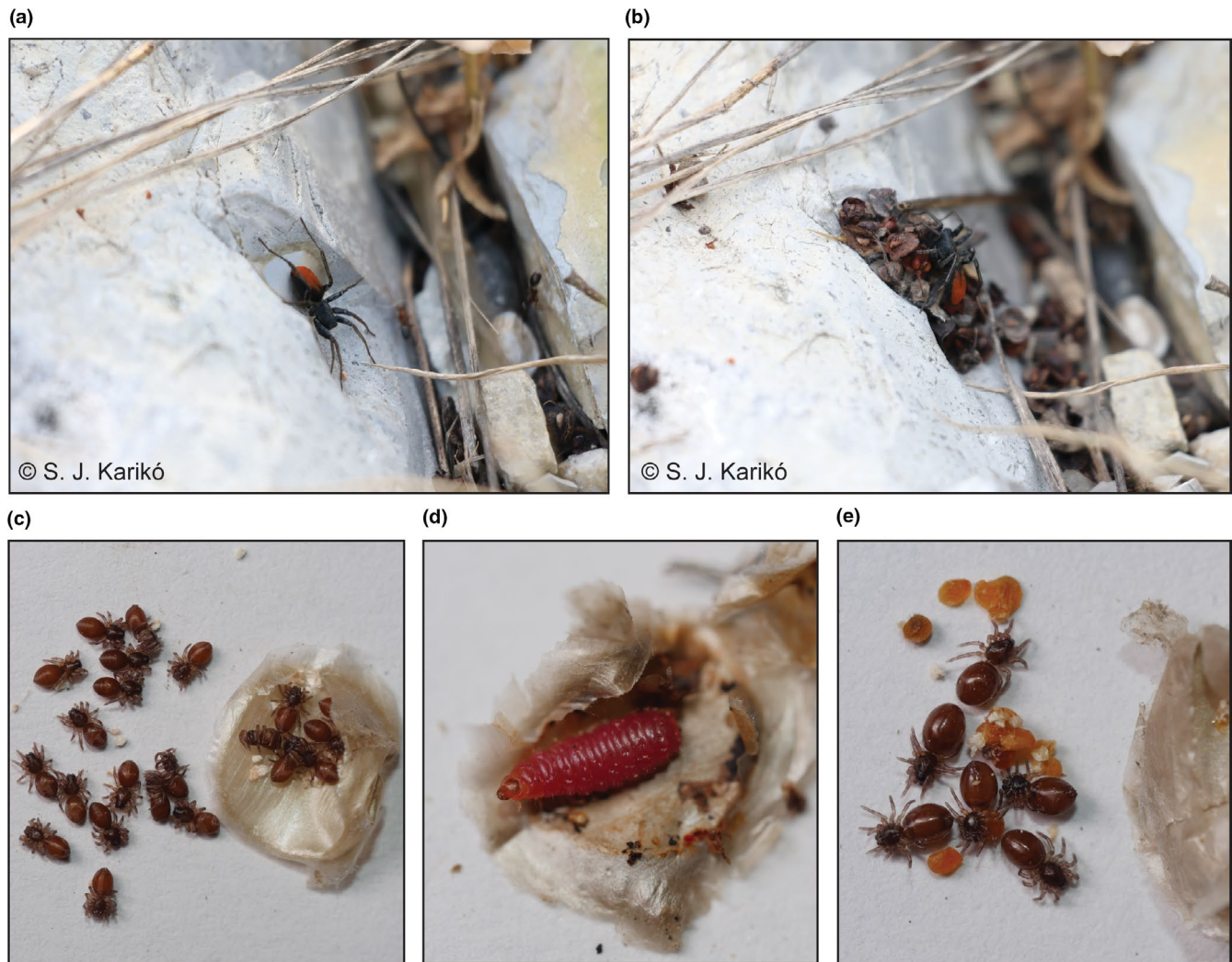
FIGURE 1 Mason spider constructing an egg sac and mound in the field and examples of egg sac contents. Mason spider constructing (a) egg sac and (b) mound at a single nest site. (c) Egg sac with healthy spiderlings. (d) Egg sac with wasp larva and total mortality of mason spider offspring. (d) Egg sac with healthy spiderlings and desiccated eggs [Colour figure can be viewed at wileyonlinelibrary.com]

duration of the treatment. The super glue was superficial; structurally reinforcing a few pieces of the nest and did not touch the egg sac. Treatment time intervals were chosen haphazardly based on field observations.

Egg sacs were randomly chosen to be collected in August ($N = 84$) or October ($N = 104$) of 2017. Egg sacs collected in August remained in place for 24–45 days (31.23 ± 5.08, $\bar{x} \pm SD$) and egg sacs collected in October remained in place for 84–109 days (94.44 ± 5.00) before they were collected. Once collected, egg sacs were transported to UC Berkeley and dissected to determine offspring mortality in each egg sac, life stage (egg or spiderling), presence of mold or desiccation, and evidence of parasitism or predation (Figure 1c-e). Eggs were determined to be dead if they were desiccated or covered in mold. Egg sacs were determined to be parasitized if wasps or wasp larva were found in egg sacs and predated if egg sac had a large hole and was empty. Dissections were done blind to any information about treatment.

2.3 | Statistical analyses

All statistical tests were performed in R v.3.6.2 (R Core Team, 2019). We performed generalized linear models to assess the effect of mounds on mortality in mason spider egg sacs overtime. Egg sacs that were predated/parasitized resulted in 100% mortality of eggs. Therefore, we analyzed mortality due to predation or parasitism (biotic mortality) and desiccation or mold (abiotic mortality) separately. We first assessed the effect of mounds on predation/parasitism of mason spider egg sacs over time by using a generalized linear model with a binomial distribution and assigned presence/absence of biotic mortality as our response variable and treatment as our predictor variable.

Next, we assessed the effect of mounds on abiotic mortality in mason spider egg sacs over time. In our model, we assigned dead/live offspring per egg sac as our response variable with the *cbind* function in R and treatment as our predictor variable. We

accounted for overdispersion in our data by using a quasibinomial distribution.

3 | RESULTS

3.1 | Behavioral description: Mound-building

Female mason spiders lay eggs and construct mounds at field sites mid-July through the beginning of September (Figure 2a). To begin, a female constructs an egg sac in a small indentation in a rock by laying silk flush with the rock. The female then lays 8–36 orange eggs (18 ± 5.1, $\bar{x} \pm SD$, $N = 151$) and covers them with another layer of silk (Figure 1a). This layer of silk is tough and papery, with an opaque pearl color, much like those described in other *Castianeira* species (Montgomery, 1909; Reiskind, 1969). Often, this is the final layer of silk in egg sac construction; however, some females will construct another thin layer of silk with an empty space (~2–4 mm) between the second and third layers of silk.

Following completion of the egg sac, the female constructs a mound (Figure 2b). To build mounds, she gathers items (e.g., pebbles, dried leaves, seeds, small sticks, arthropod parts, bird feathers) in individual collecting trips traveling between 1.25–80.66 cm (15.34 ± 11.75, $N = 462$ observed in 14 females), and returning to assemble the items into a mound held together by silk (Figure 1a,b). Shorter collecting trips were often due to females stealing material from nearby mounds rather than collecting their own. The number of collecting trips conducted by individual females to construct a mound varies. Females conduct 36–174 collecting trips per hour (102.43 ± 44.31, $N = 14$) until the mound is finished, which can take anywhere from 6 to 13 hr (Figure 2b). Based on this, female mason spiders likely conduct ~500–2,000 collecting trips to complete a mound. During all observations, we never witnessed a female spider returning to her mound following its completion. Eggs remain in the egg sac for ~2–4 weeks before they hatch into spiderlings

and overwinter as 1st or 2nd instar spiderlings in the egg sac for ~7 months. In May, mason spiders hatch out of egg sacs as 2nd instar spiderlings, leaving a molt behind in the egg sac (Figure 2a).

In our observations, mounds were regularly destroyed by weather events. Egg sacs visited one month or more following their completion were never observed with a mound. However, egg sacs remained in place through winter until spiderlings dispersed in spring (Figure 2a).

3.2 | Mound removal experiment

Mason spider egg sacs were most often predated on by field crickets (*Gryllus* sp.) and parasitized by parasitoid wasps (*Gelis* spp.). We found that mounds significantly decreased predation/parasitism. Overall, 20.2% of egg sacs ($N = 188$) were predated/parasitized and these rates differed across the four treatments. Egg sacs whose mounds were removed immediately following completion and 1 day later were the most heavily predated and parasitized (28% ($N = 50$) and 29.4% ($N = 51$), respectively) as compared to egg sacs whose mounds were removed at 10 days and >24 days (11.9% ($N = 42$) and 8.9% ($N = 45$), respectively). We found significant differences between predation/parasitism of egg sacs with mounds removed immediately and those that were never removed (control) (Table 1, Figure 3). In addition, we found that the difference between egg sacs where mounds were removed immediately and at 10 days approached significance (Table 1).

We also found that mounds significantly decrease mortality due to abiotic factors. The proportion of offspring mortality in egg sacs showed a negative relationship with the number of days mounds were present (Table 2, Figure 4). The proportion of offspring mortality in egg sacs where mounds were removed at 1 day (0.12 ± 0.23 $\bar{x} \pm SD$) and never removed (control) (0.11 ± 0.25) were significantly lower than mortality in egg sacs where mounds were removed immediately, 0.30 ± 0.35 (Table 2, Figure 4).
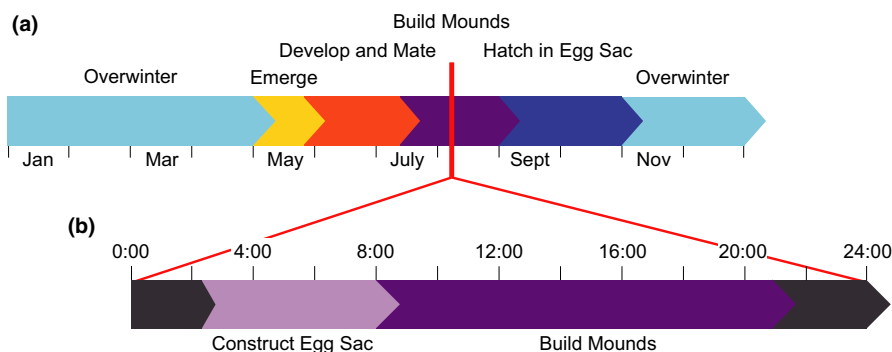

FIGURE 2 Timelines of mason spider life history and mound-building. (a) Mason spider stages of development throughout one year. Mason spiders lay eggs and build mounds in July and August. Eggs hatch into spiderlings and remain in egg sac throughout winter. In May, spiderlings emerge from egg sacs and develop into adults in early July. (b) Timeline of the building of one mason spider mound over 24 hr. Information included in timelines is generalizations based on hundreds of observations of individual spiders and egg sacs; however, variation exists in and around each stage of development [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Summary of results for generalized linear model assessing the effects of mound removal over time on the presence of predation/parasitism in egg sacs

Parameter	Estimate	SE	t	p
Day 0	−0.944	0.315	−2.999	**.003**
Day 1	0.069	0.440	0.157	.875
Day 10	−1.057	0.571	−1.851	.064
Never	−1.383	0.611	−2.263	**.024**

Note: Bolded values indicate statistical significance.
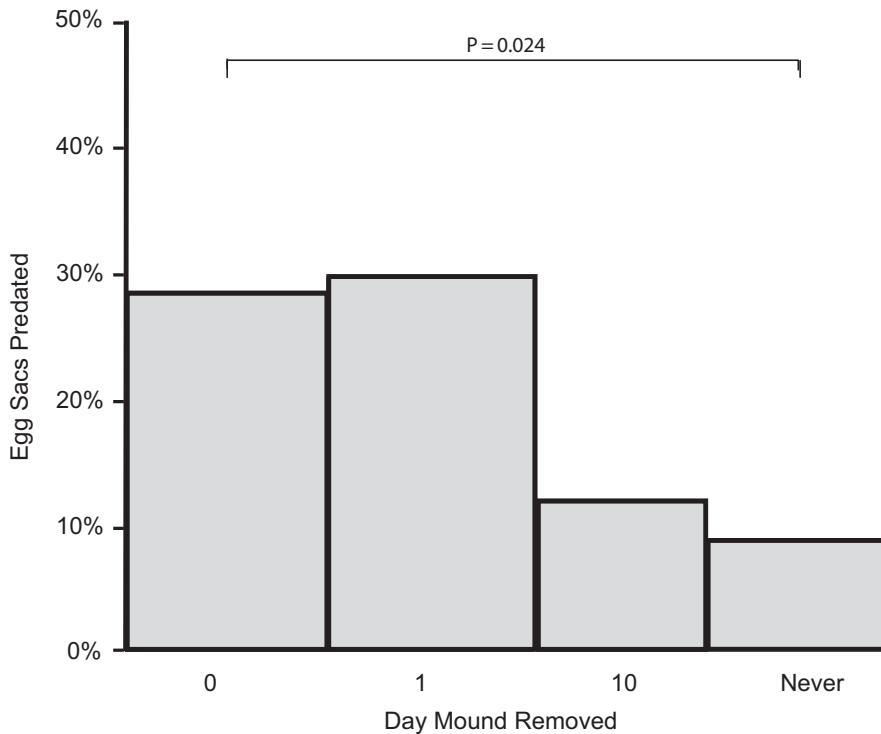
FIGURE 3 Predation/parasitism rate of egg sacs when mounds were removed from egg sacs at different time intervals following construction

first 10 days following construction, at which point egg sacs with and without mounds experience the same amount of offspring mortality. Additionally, we found that mounds protect offspring from mortality due to abiotic and biotic factors and that these benefits change differently over time.

Despite requiring a large investment of energy, we observed that mounds only remain on egg sacs for a small portion of the time that offspring inhabit nest sites. This finding contrasts with other animals that similarly invest in building protective structures but whose nests are durable enough to protect offspring throughout develop-

ment and/or until they leave the nest site (Mainwaring et al., 2014). Our study suggests that mason spider mound destruction after a short critical period (~10 days) does not result in reduced reproductive success for mason spiders due to the rapidly decreasing benefits of mounds over time.

TABLE 2 Summary of results for generalized linear model assessing the effects of mound removal over time on the proportion of abiotic mortality in mason spider egg sacs

Parameter	Estimate	SE	t	p
Day 0	−0.770	0.305	−2.520	**.013**
Day 1	−1.264	0.524	−2.411	**.017**
Day 10	−0.769	0.467	−1.646	.102
Never	−1.384	0.505	−2.739	**.007**

Note: Bolded values indicate statistical significance.

4 | DISCUSSION

Mason spiders construct elaborate nests by building mounds on top of their egg sacs, a parental care behavior that involves hundreds of collecting trips over many hours. We found that mounds are instrumental in reducing offspring mortality only for a short period of time following nest construction. This effect decreases throughout the

4.1 | Benefits of mounds against abiotic factors

The benefits of mason spider mounds are large early on, reducing the rate of predation/parasitism by 19.1% and abiotic mortality within egg sacs by 19.9%. Our experiment suggests the existence of a critical period early in offspring development where mason spider eggs are not able to survive without a mound. Across species, early development is often the period when offspring are most vulnerable to a variety of factors, including fluctuating environmental conditions, parasites, and predation (Clutton-Brock, 2001). We found that for the most part, mounds protect offspring from mortality due

Box plot representing the percentage of abiotic mortality in egg sacs when mounds were removed at different time intervals following construction

4.2 | Benefits of mounds against biotic factors
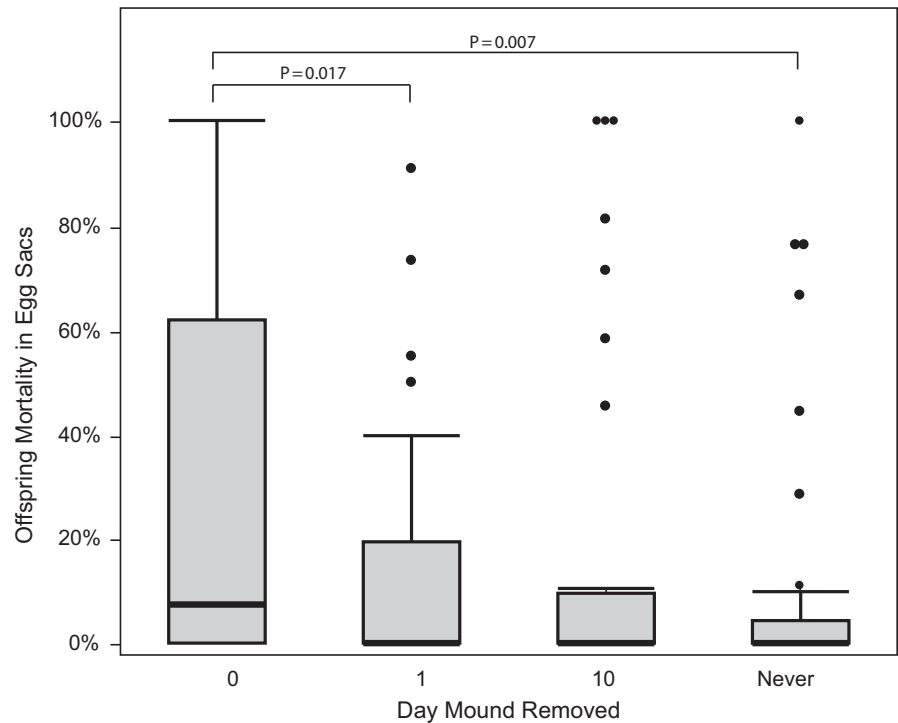
to abiotic factors in the first 24 hr following construction. Abiotic mortality in mason spider egg sacs may be due to a variety of factors including fluctuating temperatures, humidity, or exposure to UV radiation (UVR) when mounds are not present. In other spider species, eggs have been found to be especially sensitive to temperature and humidity (Hieber, 1992b; Li & Jackson, 1996; Pike et al., 2012). Mounds may provide insulation from fluctuating temperatures or humidity, which can be dramatic in alpine habitats during summer months. Additionally, mason spider eggs are laid on the tops of rocks in exposed alpine habitats with direct UVR exposure. UVR exposure can cause mortality and sub-lethal damage in the early life stages of arthropods and amphibians (Blaustein & Belden, 2003; Bothwel et al., 1994). Mason spider mounds may reduce UVR exposure of eggs early in development and could be one driver of mound-building behavior.

Interestingly, mounds do not protect mason spider offspring during arguably the most dramatic environmental conditions that they encounter, winter. In the eight months that follow mound construction, mason spider offspring remain inside egg sacs at nest sites as spiderlings and without mounds. They experience dramatic fluctuations in environmental conditions, including rain, snow, freezing temperatures, and snow melt. For arthropods, cold tolerance has been described as a critical component of their biology (Brandt et al., 2020; Lee, 2010). Future research should seek to understand aspects influencing mason spiderling overwintering, including their cold tolerance strategy, the insulating role of silk and egg sac construction, the conditions that cue diapause and the resumption of development in the spring, and the metabolic characteristics necessary for overwintering.

In addition to their abiotic benefits, mounds also protected mason spider egg sacs from predation and parasitism; however, this benefit was only present in the first 10 days following construction. Our observations suggest that egg sacs were most often predated on by crickets, although one predation event by a grouse was captured on film. Crickets have been found to be the primary predators of eggs of other arachnid species and may drive the evolution of active defense strategies of a cave-dwelling species of harvestmen (García-Hernández & Machado, 2017). The parasitoids of mason spider egg sacs were wasps in the genus *Gelis*—ichneumonids commonly known to parasitize a variety of silk covered masses including spider egg sacs and cocoons (Harvey, 2008). One hypothesis as to the mechanisms of mound protection is that mounds camouflage egg sacs from predators. To human eyes, mason spider mounds are visually conspicuous. However, *Gelis* parasitoid wasps and crickets likely detect their hosts/prey via olfactory cues (Matsumoto & Mizunami, 2000; Van Baarlen et al., 1996). In the initial days following construction, mounds might camouflage the scent of silk or eggs rendering them undetectable or increase the amount of time parasitoid wasps and other predators need to find eggs. Similarly, some birds are known to include green plant material in their nest construction, and it is thought that compounds in these materials serve as olfactory camouflage (Mainwaring et al., 2014). Overtime, the scent of silk may degrade or the silk itself may become tough to the extent that parasitoid wasps are unable to detect or penetrate egg sacs without mounds.

4.3 | Costs of mound-building

Although this study did not explicitly evaluate costs, our observations of mound-building point to a variety of costs that should be assessed in the future. First, building a mound is likely an energetically expensive activity. During mound-building, mason spiders are regularly observed stealing material from nearby mounds rather than collecting their own. Similar behaviors have been witnessed among a variety of bird species and used as indicators that nest building is energetically costly (Mainwaring & Hartley, 2013). Additionally, direct measurements indicate that birds use vast amounts of energy when transporting nesting material (Mainwaring & Hartley, 2013). Second, increased predation risk is a common cost of parental care and likely applies in this case (Ghalambor & Martin, 2002; Magnhagen, 1992; Reguera & Gomendio, 1999). Mason spiders build mounds and conduct collecting trips in mid-day in exposed areas making them and their nest location conspicuous to visual predators. One hypothesis as to the reason that mason spiders lay eggs at night is that by performing the most vulnerable and exposed parental behaviors in the dark, they reduce their risk of predation by visually-oriented predators. Finally, energy spent on the current reproductive event, laying eggs and building mounds, reduces the time and energy that could be spent on future reproductive events (Alonso-Alvarez & Velando, 2012).

4.4 | Nest durability

Our study points to multiple proximate reasons as to why mound destruction does not result in reduced reproductive success for mound builders. However, our findings also hint toward ultimate reasons for this dynamic that should be investigated further. Previous research suggests that nests that last longer are more costly to build and maintain (Abé et al., 2017). Therefore, mason spider nest (mound) durability, defined as the amount of time that a nest is able to withstand environmental conditions, may be a trait adapted to predictable environmental conditions that cause nest destruction. Similar traits of extended phenotypes, like the materials of bird bowers constructed for signaling or the shape of spider webs constructed for prey capture, have been shown to evolve or plastically respond to changing environments (Blamires, 2010; Schaedelin & Taborsky, 2009). We suggest that nest durability is also subject to selection. Nest durability may be driven by (a) the ability of young to survive independent of nests, (b) the frequency, intensity, and predictability of environmental conditions, (c) nest-site selection, and (d) nest shape and structure, including the costs and benefits of its construction and maintenance. Future work should examine these hypotheses in mason spiders but also across taxa in order to understand the different factors influencing the evolution of parental care strategies and animal architecture.

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