NATURAL HISTORY NOTE

# Destruction of Spiderwebs and Rescue of Ensnared Nestmates by a Granivorous Desert Ant (Veromessor pergandei)

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ABSTRACT: Prey species rarely seek out and dismantle traps constructed by their predators. In the current study, we report an instance of targeted trap destruction by an invertebrate and a novel context for rescue behavior. We found that foragers of the granivorous desert ant (Veromessor pergandei) identify and cooperatively dismantle spiderwebs (Araneae: Theridiidae, Steatoda spp., and Asagena sp.) During group foraging, workers ensnared in webs are recovered by sisters, which transport them to the nest and groom away their silk bindings. The presence of an ensnared nestmate and chemical alarm signal significantly increased the probability of web removal and nestmate retrieval. A subset of larger-bodied foragers participated in web removal, and 6.3% became tangled or were captured by spiders. Most animals that perform rescue behavior live in small groups, but V. pergandei colonies include tens of thousands of short-lived workers. To maintain their size, large colonies must collect enough seeds to produce 650 new ants each day. We hypothesize that the removal of spiderwebs allows for an unimpeded income of seeds on a single foraging path during a brief daily temperature window. Despite the cost to individuals, webs are recognized and removed only when workers are captured in them.

*Keywords*: Theridiidae, web architecture, group foraging, group size, group defense.

#### Introduction

Nonhuman animals build a remarkable variety of preycapture devices. While some traps are improvised (Sanz et al. 2009), most are honed by an evolutionary arms race between predator and prey. The greatest variety of traps are engineered by invertebrates, including the mucus nets of polychaete worms (Flood and Fiala-Médioni 1982), pitfall traps of antlions (Fertin and Casas 2006), aquatic sieves of caddisflies (Engster 1976), fungus-lined gallery traps of ants (Dejean et al. 2005; Schmidt and Dejean 2018), and the thousands of silken nets, snares, funnels, sheets, trap-

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doors, and bolases of spiders (Eberhard 1990). The defensive strategies associated with trap architecture are no less elaborate. For example, moths evade orb webs by adopting a vertical flight path and shedding detachable wing scales (Eisner et al. 1964; Nentwig 1982), while trap jaw ants (*Odontomachus brunneus*) escape antlion pits by snapping their mandibles at the ground surface and propelling themselves upward (Larabee and Suarez 2015).

Although prey species exhibit a wide range of escape and avoidance tactics, few seek out and destroy the structures designed to capture them (Ohashi and Matsuzawa 2011; Than 2012). Likewise, only a handful of highly social organisms participate in the rescue of conspecifics captured in traps or otherwise imperiled (Hollis and Nowbahari 2013). Rescue behavior is a rare form of helping behavior defined by the risk to both the victim and the rescuer, the suitability of the rescue attempt to the circumstances, and the absence of an immediate reward for the rescuer (Nowbahari and Hollis 2010). Most species that perform rescue behavior form comparatively small groups with high-value individuals (Frank and Linsenmair 2017), like those of chimpanzees, white-faced capuchin monkeys (Vogel and Fuentes-Jiménez 2006), Seychelles warblers (Hammers and Brouwer 2017), and Atlantic bottlenose dolphins (Siebenaler and Caldwell 1956).

Rescue behavior has been observed in less than five natural contexts across more than 13,000 ant species. Most commonly, nestmates locate and exhume sisters buried by collapsed tunnels or retrieve sisters from the pitfall traps of predatory antlions (Czechowski et al. 2002). Foraging Matabele ant workers (*Megaponera analis*) retrieve injured sisters following group raids on termite colonies. Clinging termites are later removed, and wounds are treated by sisters in the nest (Frank et al. 2017, 2018). Like dolphins and chimpanzees that perform rescue behavior, Matabele ants form relatively small colonies, where the value of each individual is high and the birth rate is low, at just 13 ants per day (Frank et al. 2017).

In the current study, we report an instance of systematic trap destruction in an invertebrate and a novel context for

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rescue behavior in a granivorous desert ant. We found that foragers of *Veromessor pergandei* locate and dismantle webs built by myrmecophagous spiders (*Steatoda* spp. and *Asagena* sp). Workers then retrieve ensnared sisters and groom away their silk bindings. Unlike Matabele ants, *V. pergandei* form large societies with a birth rate of up to 650 ants per day and a peak foraging force of nearly 30,000 individuals, each with a foraging career no longer than 18 days. In contrast to other animals that perform rescue behavior, *V. pergandei* foragers are comparatively "disposable," as colonies may replace as many as 34,000 during their peak foraging month and 230,000 in a single year, the equivalent of 470 grams of dry biomass (Kwapich et al. 2017).

*Veromessor pergandei* is a group forager with polymorphic workers that travel together to different seed foraging sites each day. In the early morning, workers select a foraging direction and depart en masse in a single column (rarely two). Workers may travel as a group for more than 40 m before fanning outward in search of seeds (Plowes et al. 2013). When successful, each forager returns to the distal end of the chemically reinforced trail and carries a single seed back to the nest (Plowes et al. 2014). Although *V. pergandei* is endemic to the Sonoran and Mojave Deserts, it is heat intolerant and prone to desiccation (Johnson 2000). Therefore, individuals race to complete multiple foraging trips within a narrow temperature window, found for as little 2 h a day (Bernstein 1974; Hunt 1977).

Given the massive scale of foraging, the brief tenure of foragers, and impermanence of foraging trails, it is puzzling that *V. pergandei* colonies invest in the destruction of spiderwebs and rescue of individuals. The current study describes how ants identify webs and remove them and considers the conditions necessary for the evolution of rescue behavior in large societies with short-lived individuals.

#### Methods

#### Behavior in the Field

We recorded the interactions of 95 *Veromessor pergandei* workers with 29 webs constructed by adult *Steatoda* spp. and *Asagena* (=*Steatoda*) sp. spiders. Happenstance observations of web destruction and retrieval of ensnared nestmates were made for 25 unique colonies during detailed observations of *V. pergandei* foraging column formation in two Sonoran Desert populations and one Mojave Desert population (January–August, 2015–2018). Sites were located in South Mountain Regional Park, Phoenix, Arizona; McCartney Road, Casa Grande, Arizona; and Borrego Springs, California.

To determine whether web destruction was context specific, we assessed three binary conditions from video recordings and observations in the field: (1) the presence or absence of nestmates in the web, (2) the presence or absence of a spider in the web, and (3) the presence or absence of foraged seeds tangled in the web. Some webs were positive for more than one characteristic (i.e., a captured nestmate and a spider might occupy the web at the same time). Empty webs received zeros for all three dichotomous predictors (representing the model's intercept). Web removal was defined by prolonged biting and pulling of silk threads by one or more ants, leading to a loss in web structure. Samples were independent and assessed using a binomial logistic regression. To account for quasi separation of the data (monotone likelihood), we followed established methods to produce finite parameter estimates by reducing the bias of maximum likelihood estimates (R ver. 3.3.2, package blrgm; Heinze and Schemper 2002).

To determine whether certain workers were more likely to remove webs, we identified whether ants that removed webs were seed laden or unencumbered at the time of web discovery (n = 95). Veromessor pergandei workers are polymorphic, ranging from 3.5 to 8.4 mm in length (Davidson 1978). Ants that participated in web removal were classified as small (head widths, 0.5–1.0 mm), medium, or large (head widths, 1.4– 1.9 mm) by comparing head width to a size standard printed on clear acetate calibrated with a wedge micrometer. Size categories were defined across colonies and seasons for more than 1,600 individual ants in previous studies conducted at South Mountain and Casa Grande (Kwapich et al. 2017, 2018).

Some ant species prune vegetation around the nest entrance or remove objects from the path of foraging (Bochynek et al. 2016). *Veromessor pergandei* is not known to clear foraging routes (Kwapich et al. 2017). However, to determine whether foragers respond to novel objects, we wrapped 5 cm of nylon silk (a synthetic polymer) around two 3-cm-high wooden toothpicks and inserted them directly into the active foraging column, so that the nylon thread contacted the ground at a diagonal. Objects were monitored for 1 h for any instances of biting, lunging, prolonged inspection, or removal (n = 15 field colonies, one trial per colony).

# Nestmate Signaling

To determine how foragers detect webs, we presented field colonies with combinations of stimuli associated with webs and captured nestmates in two complimentary experiments. Colonies were offered a single replicate of each stimulus in random order at 15-min intervals. Each stimulus was placed perpendicular to foraging traffic 200–210 cm from the margin of the nest mound. Five minutes after presenting each stimulus, the number of ants presently engaged in biting, pulling, or directed mandible gaping and lunging was tallied.

In the first experiment, we investigated potential sources of a chemical alarm signal. An unidentified compound in the mandibular glands is thought to elicit an alarm-defense response (Wilson and Regnier 1971) in *V. pergandei* workers (Blum et al. 1969; Wilson and Regnier 1971). It has been claimed that benzaldehyde is one of the components of the mandibular glands (Blum et al. 1969); however, Hölldobler et al. (2013) found that this compound was wrongly attributed and in fact originates from the pygidial gland in the gaster. In *V. pergandei*, trail-following behavior is released by 1-phenyl ethanol from the poison gland found in the gaster (Plowes et al. 2013), while *n*-tridecane, one component of the pygidial gland, acts as an excitement-recruitment pheromone during trail formation (Hölldobler et al. 2013).

In our experiment, nestmate responses to crushed heads (mandibular gland) and crushed gasters were compared using a Wilcoxon signed-rank test that accounted for samples being paired by colony and the nonparametric nature of the data (n = 30 field colonies, 28 pairs with rank differences). Using clean watchmaker's forceps, the head (n = 30) and mesosoma were separated from the gaster (n = 30) of one chilled ant per colony and crushed with separate, blunt-ended wooden toothpicks. Control toothpicks pressed against a damp cotton ball (n = 30) received zero responses from workers and were subsequently dropped from statistical analyses.

In the second experiment, we presented stimuli including wooden toothpicks wrapped with (1) clean silk, (2) silk and a freeze-killed (dummy) nestmate, (3) silk used to restrain an alarmed worker against a glass plate for 3 s, (4) silk marked with the contents of one crushed head, and (5) silk with a freeze-killed (dummy) nestmate marked with the contents of a crushed head (n = 16 field colonies). We used fresh silk from the black widow spider (*Latrodectus hesperus*), reared on a diet of crickets (*Acheta domesticus*). We chose silk from the closely related black widow because *Steatoda* were reluctant to build webs without first interacting with ants (which could contaminate the silk). The frozen dummy workers in our experiments were rapidly immobilized after being coaxed onto a blade of vegetation and moved to a block of ice for 15 min.

Differences in the number of workers responding to stimuli after 5 min were compared with a zero-inflated, Poissondistributed generalized linear mixed model (ZIP GLMM) that included treatment (stimulus) as a fixed effect and colony identity as a random effect (R package glmmTMB). We chose to use a Poisson GLMM because our response variable (number of ants attacking) was a count taken over a fixed interval. The zero-inflated model accounted for low worker responses to certain stimuli, which resulted in numerous real zeros in the data set (Brooks et al. 2017). Data from observations of web removal and worker responses to experimental stimuli have been deposited in the Dryad Digital Repository (https://dx.doi.org/10.5061/dryad.412jp56; Kwapich and Hölldobler 2019).

#### Rescue Behavior

To study cues related to rescue behavior, we presented four field colonies with freeze-killed nestmates wrapped in silk only and freeze-killed nestmates wrapped in silk marked with the contents of one crushed head. Wrapped nestmates were placed in a row in alternating order, 200 cm from the colony's nest entrance (n = 20 silk only, 20 silk and crushed head, four colonies). We monitored the corpses for 2 h and recorded whether each corpse was carried into the nest and the length of time between corpse placement and retrieval by nestmates.

In the laboratory, we allowed Steatoda sp. to capture ants and construct webs on foam and wire stands in plastic sandwich boxes. After capturing ants, spiders were removed and structures containing webbing and captured ants were presented to two colony fragments housed in 30 × 200-cm laboratory arenas (see app. A for additional details; apps. A, B are available online). The process of web removal and nestmate rescue was documented outside and inside the glass-topped observation nest located at one end of the arena (n = 8)webs). We observed that some ants were bitten but not eaten by spiders and subsequently retrieved from webs by nestmates. To determine whether bitten ants recovered in the nest, we returned individuals that were wrapped and bitten by captive Steatoda to groups of 50 nestmates in the laboratory. We then monitored bitten ants for signs of recovery overnight (n = 6 workers).

#### Quantifying the Costs and Benefits of Web Removal

Like many ant species, *V. pergandei* workers progress through a sequence of labor roles as they age, ending with foraging outside the nest. All workers become foragers, and foragers do not revert to previous jobs prior to death. Therefore, repeated measurements of a colony's forager population size and turnover rate can provide reliable estimates of the total number of ants produced over one annual cycle. We considered the costs and benefits of web removal using known values for forager longevity (18 days), forager population size, and annual forager production taken from repeated Lincoln index mark-recapture events spread across one annual cycle for 14 *V. pergandei* colonies in our South Mountain focal population (see app. B for additional details; Lincoln 1930; Kwapich et al. 2017). Colonies were monogynous and contained one to seven patrilines (Kwapich et al. 2017).

# Results

# Description of Webs and Capture in Nature

Shortly after sunrise, male and female *Stetoda* spp. and *Asagena* spp. were found wandering the desert floor. On contact with *Veromessor pergandei* foraging trails, spiders constructed small webs above or adjacent to the column of ants (63%) or on the nest mound (38%), with as many as seven

gumfoot threads anchored to the ground and additional threads secured between vegetation, sticks, or rocks 2–7 cm above the ants' path (n = 29 webs). When a web was contacted by a passing ant, the resident spider descended rapidly and began reeling in its prey (video 1; videos 1–6 are available online). Ants were sometimes flipped upward and suspended into the spider's web after contacting a taut line of silk. Captured ants were wrapped in silk and then repositioned and wrapped again with special attention to the legs. After wrapping, ants were (1) bitten repeatedly on the legs and then isolated until immobile before being consumed, (2) bitten and isolated/abandoned, or (3) isolated without being bitten.

When feeding was completed, spiders left the ant in the web or dropped it to the foraging column below (video 1). Between 1 and 8 corpses or captured ants were observed with successful webs (n = 19 webs). After capture, both active and immobilized ants were suspended above the foraging trail, typically beyond the physical reach of passing nestmates. Spiders were easily disturbed by interfering ants or foragers whose seeds became tangled in silk and temporarily or permanently abandoned existing webs to build additional snares along the foraging route. During the day and overnight, we found spiders sheltering under stones adjacent to *V. pergandei* mounds, where they also placed their egg sacs.

# Removal of Webs by Ants

The presence of an ensnared nestmate significantly increased the probability of web removal by ants under natural conditions (binomial logistic regression, z = 2.36, P = .018, n = 29 webs; table B1; videos 2, 3; tables B1, B2 are available online). Webs that were empty or that included



**Video 1:** Still photograph from a video (video 1, available online) showing a female spider (*Steatoda* sp.) building her web adjacent to a *Veromessor pergandei* foraging column. The spider discards a previously consumed ant and then captures another.



Video 2: Still photograph from a video (video 2, available online) showing several foragers removing a web containing a spider and ensnared nestmate (*upper middle*), built near the nest mound. One web remover becomes temporarily tangled in the web. Other ants struggle to free their seeds from the web.

a spider and/or tangled seeds were rarely destroyed unless a captive nestmate was also present. Only three of 19 webs were destroyed without a captured worker present. The presence of a seed-tangling event significantly decreased the likelihood of targeted web removal (binomial logistic regression, z = -2.16, P = .031; table B1).

Foragers that engaged in web removal faced personal risk, as 6.3% of rescue attempts ended in the rescuer engaging with or being captured by a spider (6 of 95 web removers). Workers that removed webs were unencumbered by seeds, and 56.8% ranked in the top third of the body size distribution of the polymorphic workforce. Medium-sized workers participated to a lesser degree (41%), and the smallest workers were observed participating only twice (n = 95 web removers). On average, only six (SD, 5) of thousands of passing workers responded to a web containing a trapped nestmate (range, 1–21 ants; 19 webs removed).

Workers that did respond to webs displayed a variety of agonistic behaviors (video 2). Most moved rapidly, pausing to sweep their antennae upward, before lunging toward the web with mandibles gaping and forelegs straightened. When interacting with a web, ants were also observed pulsating their gasters and turning rapidly to seize and hold approaching nestmates for a fraction of a second. These behaviors excited additional nestmates, which occasionally joined in web removal.

The process of web destruction proceeded as workers removed each silk thread anchored to the ground or surrounding vegetation and stones. On contact, a silk line was gripped between the ant's mandibles at a distance of approximately one body length from the anchor point. The ant then walked slowly backward, pulling the silk outward until it bowed into a taut V shape between the anchor point



**Video 3:** Still photograph from a video (video 3, available online) showing numerous foragers removing parts of a web constructed over their foraging column following a mating fight. A spider is present in the upper left of the screen, and several ant corpses can be seen on the ground and in the web. Web removers stand and walk on parts of the spider's web as they remove it.

and upper connection (fig. 1). When the ant could no longer pull the silk any farther, the thread was released and the process was repeated until the anchor point was detached. For each silk thread, this process continued until there was no more tension in the web and silk lines hung in tangled wisps. Ants were capable of walking on silk anchored to rocks and vegetation and did so in the later stages of web removal.

When a web became fully detached, strands that clung to ant mandibles and legs were consequently dragged through debris and dirt until they were no longer sticky. The time needed to remove a web varied from just under 30 min to more than 2 h in one laboratory trial (n = 8 trials, 2 laboratory nests). In most cases, participants were unwavering in their attention to web removal, only occasionally breaking away and then looping back to the web (video 4). Not all attempts to destroy webs or rescue nestmates were successful in the field. Of the 19 webs that were attacked, four were abandoned prior to complete removal. Three of these instances correlated with the general cessation of foraging associated with air temperatures above 31°C. In these cases, two dead ants were removed and one live ant was successfully separated from the remaining webbing. In the fourth case, a single web remover was captured by a spider in the web near the end of the foraging period, and no nestmates responded.

# Tangled Seeds

The seeds carried by inbound foraging ants became tangled in silk in 24% of webs (7 of 29 webs). Inbound foragers carrying

seeds never contacted or removed silk and did not abandon seeds tangled in webs until temperatures drove them into the nest. Therefore, workers invested in pulling on a tangled seed for the remainder of the foraging period rather than taking multiple foraging trips like their nestmates. In some cases, upward of 10 ants could be seen pulling on their tangled seeds or repeatedly releasing a seed, wandering in loops and returning to pull on it again (video 5). Seed tangling resulted in congestion of foraging traffic, causing a sprawl of inbound and outbound workers forced off the established pheromone trail that marked their path.

# Signaling by Captured Ants

We found that web removal is not a type of vigilance behavior directed toward novel objects, debris, or polymers (like nylon or silk) in the foraging column. When novel objects made of nylon and wood (n = 15 colonies, one trial per colony) were placed directly into the foraging trails in the field, there were zero instances of prolonged inspection, biting, mandible gaping, or pulling on any part of the object.

Fresh silk and fresh silk wrapped around a dummy nestmate received significantly less aggression than silk that restrained an alarmed worker for 3 s (ZIP GLMM; fresh silk: z = -3.69, P = .0003; silk wrapped around a dummy nestmate: z = -3.71, P = .0002; table B2). Only one ant across all 16 trials attacked fresh silk. On average, less than one ant per trial attacked fresh silk wrapped around a dummy nestmate (0.76; SD, 0.90; n = 16 trails). In contrast, silk that restrained an alarmed worker and silk wrapped around a dummy marked with head contents both provoked high levels of aggression (ZIP GLMM, z = 1.63, P = .10), while silk marked with crushed head contents elicited slightly more aggression than restraint silk alone (ZIP GLMM, z = 2.21, P = .03). An average of 2.5 (SD, 1.4; n = 16) workers per trial attacked silk that previously restrained an alarmed worker, while 3.93 (SD, 1.91; n = 16) ants per trial attacked silk marked with crushed head contents and 3.5 (SD, 1.5; n = 16) ants per trial attacked silk wrapped around a dummy nestmate marked with crushed head contents (fig. 1).

In the field, the contents of crushed heads (mandibular gland) received significantly more aggression than crushed gasters (Wilcoxon signed-rank test, 28 ranked pairs, z = 4.54, P < .0001). On average, 2.5 (SD, 1.7; n = 30) and up to seven ants per trial attacked toothpicks marked with contents of a nestmate's crushed head, while less than one (0.17; SD, 0.46; n = 30) worker per trial attacked toothpicks marked with gaster contents after 5 min. Together, these findings suggest that ants are not innately aggressive toward silk but that a chemical alarm defense signal, likely originating from the mandibular gland, can release agonistic behavior when bound to silk, even in the absence of a nestmate.



**Figure 1:** *Top*, two nestmates pull on webbing surrounding an ensnared sister. *Bottom left*, three large foragers inspect a freeze-killed nestmate (dummy) marked with mandibular gland/head contents. *Bottom right*, a worker pulls on the final threads of a dismantled *Steatoda* sp. web in the foraging column.

#### Rescue of Ensnared Nestmates

In most cases, ensnared workers were suspended above the reach of nestmates until the final steps of web removal. On contact with a tangled nestmate, workers pulled at her remaining silk bindings. Most workers then freed themselves from the silk wrapped around their legs. In six natural instances, we observed passing ants collect a fresh corpse or struggling nestmate wrapped in silk and return with it to the nest mound in the field.

Similarly, silk-wrapped dummies marked with mandibular gland contents were retrieved and brought to the nest in 17 of 20 field trials (85%). Of the marked dummies that were retrieved by nestmates, carrying began 45 s to 46 min after placement (mean, 20.07 min; SD, 14.20 min). Four of the rescued dummies were carried home in steps by different nestmates. Three of 17 dummies were left on the nest mound rather than being brought inside and remained there at the end of the 2-h observation period. In contrast, none of the 20 unmarked dummies wrapped in silk were retrieved by 2 h, although four were moved short distances in either direction on the foraging column.

In the laboratory, behavior toward rescued workers could be observed inside nest boxes with glass lids. Workers were rescued in all eight laboratory trails with *Steatoda* webs and as many as five ants groomed each rescued nestmate, meticulously removing the silk wrapping that had been applied by the spider (video 6). Once removed, the silk was masticated



**Video 4:** Still photograph from a video (video 4, available online) showing highlights from the middle of a web removal and rescue event in the laboratory that took more than 2 h to complete (speed is 1.5× regular).

and antennated without any displays of aggression or alarm, such as mandible gaping or rapid movement. Dead workers were not cannibalized, and silk was not consumed. Both were later brought out to the trash pile. Live, unbitten workers conducted extensive personal grooming after being freed. Workers bitten by spiders did not recover from their bites even when placed with 50 nestmates overnight in the laboratory (n = 6).

#### Discussion

In ant species that perform rescue behavior, captured nestmates often communicate their status and location using chemical signals (Crewe and Fletcher 1973; Frank et al. 2017) or by stridulating (Markl 1965). We show that rather than being innately aggressive toward silk or novel objects, Veromessor pergandei workers attack webs and rescue nestmates in response to chemical alarm signals from captured sisters. Thus, despite the potential cost to individuals, webs are recognized and removed only when workers are ensnared in them. Rescue behavior is typically associated with longer-lived animals that form small groups, where the loss of one individual may substantially reduce group size. Although V. pergandei forms large societies, we propose that limited access to resources and a high rate of worker turnover can also lead to investment in measures like web destruction and rescue behavior.

#### Costs and Benefits of Web Removal

The maintenance of group size has been suggested as an important driver for evolution of rescue behavior in social species (Frank et al. 2017). For *V. pergandei*, maintaining large

numbers of foragers is so essential to colony survival across years that colonies reduce worker body size rather than making fewer workers during lean months (Rissing 1987). Large, reproductively mature nests must convert seeds into an average of 650 new ants per day to balance a daily loss of 6.4% of the standing forager population. Large colonies, headed by a single queen, rear and replace as many as 34,000 foragers in their peak foraging month and up to 230,000 foragers during a single year (Kwapich et al. 2017).

We observed webs with up to eight captured workers and up to 10 workers struggling to free tangled seeds. Although one forager represents as little as 0.0038% of the standing foraging force in the largest colonies (25,891 foragers) and 0.31% of the foraging force in the smallest colonies (319 foragers; Kwapich et al. 2017), we estimate that losses accrued over time due to spider predation may have significant impacts on seed income and colony success. For example, if a forager were to survive the typical 18 days and successfully collect two seeds per day, losing the income of five new foragers a day would amount to a loss of 65,700 seeds annually (1,825 per year, 36 seeds per ant). This is true despite an exceptional standing forager population size (median, 10,337).

In addition to rescuing living workers, dead or permanently immobilized nestmates were also retrieved from webs. While retrieval of a dead nestmate seems counterintuitive at the individual level, we show that it is the initial release of an alarm pheromone that stimulates web destruction. Web removal prevents seed tangling and allows for unobstructed foraging for the rest of the foraging force. Workers that encounter webs while carrying seeds pulled on their seeds for the remainder of the forager period without destroying the offending web, reducing the number of subsequent trips that could be taken



**Video 5:** Still photograph from a video (video 5, available online) showing seeds being carried by inbound foragers becoming tangled in a web built across their foraging column. As foragers pull on tangled seeds, the spider moves throughout its web.



Video 6: Still photograph from a video (video 6, available online) showing the following. Part 1: A freeze-killed worker marked with mandibular gland contents and wrapped in silk is carried to the nest by a sister alongside inbound seeds. Part 2: Inside a laboratory nest, large-bodied workers groom a live nestmate retrieved from a web. Part 3: A dead nestmate, bitten by a spider and wrapped in silk, is collected and carried into a laboratory nest. Inside the nest, workers inspect and groom the worker.

that day and the annual seed income for the colony. The benefits of capture accrued at the colony level may, therefore, outweigh the risks associated with capture at the individual level.

# Rescue Behavior

Hollis and Nowbahari (2013) propose that four criteria must be satisfied to classify helping as rescue behavior. First, the victim must be in immediate physical danger. *Veromessor pergandei* workers ensnared in webs are in danger of being bitten and consumed by the spider that constructed the web. Likewise, *V. pergandei* is heat intolerant, and abandoned workers desiccate rapidly outside their early morning foraging window. Second, the rescuer must place itself at risk. By contacting the sticky web and freeing lines of silk, *V. pergandei* rescuers were captured by spiders or ensnared 6.3% of the time.

Third, the rescue must be suited to circumstance of the victim. In *V. pergandei*, the biting and pulling of silk, rather than the scaffolding holding the web, demonstrates a direct interaction with the object of restraint rather than a response to novel objects or generalized aggression. Fourth, the rescue must not be immediately rewarding to the rescuer (beyond the benefits of relatedness). When a *V. pergandei* worker frees a sister, there is no indication that she receives additional protection or reward, nor does cannibalism occur. While *V. pergandei* satisfies the criteria outlined above, we agree that rescue behavior need not include

an element of immediate physical peril but may be driven by delayed costs and benefits, such as perennial colony survival or maintaining the minimum number of workers necessary to invest in annual reproduction (Frank and Linsenmair 2017).

#### The Evolution of Web Removal

Spiders target prey species by building webs with chemical lures, attractive coloration, camouflage, patterns of silk tension and stickiness, and even static electricity (Kenneth 1988; Benjamin and Zschokke 2003; Théry and Casas 2009; Vollrath and Edmonds 2013). Social prey species present a special problem for predatory architects, which must account for additional vigilance and aggression from group members (Hale et al. 2018). The spiders in our study exploit the massive foraging columns of V. pergandei by constructing temporary webs that may persist less than 2 h on the desert floor (Bernstein 1974; Hunt 1977). The spiders' adaptation to a large but ephemeral resource is met by an unlikely defense on the part of its prey. Veromessor pergandei workers lack the ability to spray chemical compounds or sting like other sympatric seed harvesting species; instead, captured V. pergandei foragers communicate the location of webs and wait to be rescued. At the colony level, most seed-harvesting ant species engage in complex web detection avoidance tactics, such as arresting foraging for a period of days, sealing the nest entrance, or relocating the nest entrance a meter or more away (Hölldobler 1970; MacKay 1982).

In *V. pergandei*, components of the silk removal sequence were likely co-opted from other areas of the forager's typical repertoire. The grasping and pulling processes associated with disconnecting silk from its anchor point resembles seed removal from food plants, a behavior also disproportionally undertaken by large-bodied workers (Rissing 1987). Silk removal is also coupled with agonistic behaviors, such as forward jerking movements with open mandibles, seen in forager interactions with nonnestmate conspecifics. Seed-encumbered workers never respond to webs except to tug directly on their tangled seeds. These findings suggest that there is significant variation in alarm response thresholds among workers and that web removal is secondary to seed-retrieval behavior in the ants' hierarchy of tasks.

In a series of laboratory studies, researchers demonstrated that various ant species bite and pull at nylon restraints used to fasten nestmates to cardstock (Nowbahari et al. 2009). Similarly, the weaver ant (*Oecphylla smaragdina*) was shown to either rescue or cannibalize workers experimentally wrapped in silk, depending on distance from the nest in the field (Uy et al. 2019). The observed behavior toward nylon restraints and silk-wrapped workers resemble the natural web removal repertoire of *V. pergandei* and hints that a wider variety of ants may attempt web removal in nature. Weaver ants may

be particularly adept at web removal because of their tendency to manipulate larval silk as a building material (Uy et al. 2019). While ant species like *Pogonomyrmex badius* are known to approach nestmates captured in webs, they are soon overwhelmed by the sticky threads and become victims themselves (Hölldobler 1970, 1976). The success of *V. pergandei* may therefore be related to the disposable nature of the snares built to capture them or their special ability to grip and walk on parts of *Steatoda* and *Asagena* webs.

#### Conclusions

We propose that an important driver for the evolution of trap destruction in V. pergandei was its tendency to participate in large-scale group foraging on one or limited routes, where foraging is temporally constrained due to temperature and opportunity. Unlike many Pogonomyrmex seed harvesters that face spider predation (Hölldobler 1976), V. pergandei colonies establish a single novel route each day. Successfully redirecting such a massive, chemically reinforced trail in response to spiderwebs would be unlikely. Likewise, circumventing spiderwebs could increase individual trip distances beyond 40 m in length. This might be costly, as increased foraging distance in this species is correlated with increased seed selectivity and handling time, leading to fewer individual trips per foraging period (Rissing and Pollock 1984). Frank and Linsenmair (2017) propose that group foraging could also be an important precondition for the evolution of rescue behavior because ants must be abundant enough on routes to encounter injured nestmates. This is certainly true of V. pergandei, where an average of just six out of thousands of passing foragers respond to alarmed nestmates in webs.

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