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SHORT COMMUNICATION

Home on the range: a pilot study on solifuge (Solifugae: Eremobatidae) site fidelity at Rocky Mountain Arsenal National Wildlife Refuge

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Abstract. Many animals, including many arachnids, return to an established "home" after an active period. Although desert-adapted solifuges shelter from the sun in retreats, it is unknown if these solifuges "home" to and re-use the same retreats over multiple consecutive periods. We sought to investigate whether individual solifuges exhibit site fidelity (philopatry) and could be found repeatedly within the same small geographic area using a simple mark-and-recapture study design. Over the course of the seven-day study period, nine of 46 solifuges were recaptured once, and two were recaptured a second time, with an average of 4.17 m between encounters. This rate of recapture is suggestive that solifuges remain in or return to the same geographic area over some period of time – a prerequisite for homing behavior. Further investigation is warranted to establish if solifuges are repeatedly using the same retreats, and if so, how they are navigating during homing.

Keywords: Camel spider, mark-and-recapture, philopatry.

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Solifuges, members of the sixth largest order of Arachnida (Harvey 2003), are a poorly understood group, largely due to the difficulty of capturing sufficient numbers of specimens and maintaining them in a laboratory setting for controlled study. Consequently, many of the most basic aspects of solifuge biology remain elusive, with existing knowledge primarily derived from field observations, and only two successful laboratory studies (Muma 1966b; Punzo 1998a). Recent improvements in field collection techniques have improved capture yield of solifuges by exploiting their positive phototactic behavior (Cushing & González-Santillán 2018; Graham et al. 2019), enabling experiments in the field and investigations of behavioral and ecological questions, as in the present study. Among the wealth of enigmatic components of solifuge biology are their dispersal capabilities, which may be determined by constant or intermittent travel, or constrained by site fidelity (also known as philopatry) through returning to or remaining in a particular geographical area.

Like many desert-adapted animals, most solifuge species are nocturnal and spend the daytime hours sheltered from the desert sun. Solifuges construct retreats by burrowing under rocks, vegetation, ungulate feces, or in open substrate (Cloudsley-Thompson 1961, 1977; Muma 1966a), which are used during ecdysis, digestion, overwintering, and the deposition of eggs (Muma 1966b). There is some evidence that, in at least males of *Ammotrechula peninsulana* (Banks, 1898), solifuges reuse burrows over at least three consecutive nights (Gore & Cushing 1980). It is hypothesized by Gore & Cushing (1980) that the re-use of burrows is an optimal strategy in that animals avoid expending energy constructing a new burrow after each active period. If the re-use of burrows is an optimal behavior, it implies the establishment of a home range, a geographical area in which an organism constrains its activity (Ford 1983; Polis et al. 1985). Naturally, re-use of burrows requires an organism to be able to "home" back to a focal point (e.g., a burrow or nest), which would involve one or multiple mechanisms of navigation. Homing behavior (namely path integration) is found in multiple spider, scorpion, and whip-spider taxa, and is extensively reviewed in Gaffin & Curry (2020). Site fidelity and burrow re-use in Solifugae would indicate the evolution of homing behavior in yet another arachnid group.

The purpose of this study was to determine if individuals in a population at Rocky Mountain Arsenal National Wildlife Refuge (RMANWR) exhibit site fidelity, which is inferred if marked individuals are recaptured at least once after the initial encounter. Establishing philopatric behavior is a starting point for future investigations of homing and navigational mechanisms in Solifugae.

We attempted to replicate the methodology of Gore & Cushing (1980), which investigated solifuge burrow re-use in New Mexico. Our study was carried out in RMANWR in Commerce City, Colorado (Fig. 1B). Located northeast of Denver, RMANWR comprises nearly 16,000 acres, the majority of which is prairie habitat consisting of native short grass prairie vegetation. We initially chose to sample around the Refuge Visitor Center due to the presence of external building lights, as we expected it would offer the best opportunity to encounter solifuges due to their apparent positive phototactic behavior (Pocock 1897; Turner 1916; Turk 1947; Cloudsley-Thompson 1961, 1977; Punzo 1998b; Catenazzi et al. 2009; Conrad & Cushing 2011; Belozerov 2013; and tested in Graham et al. 2019). However, due to early closure of RMANWR because of CoViD-19 restrictions, the external building lights remained off for the entirety of the study period. In lieu of building lights, we placed Coleman lanterns atop camera tripods, approximately 2.5 m from the ground, at three separate locations (Fig. 1A). Sampling locations were scouted on 30 June, and after finding seven solifuges (data not included here), we began our 7-night study period the following night on 1 July. Sampling efforts began at approximately 20:30 (within minutes of sunset) and ended generally between 01:00 and 01:30. Sampling was constrained to the natural areas within 100 m of the visitor center, excluding the human-made structures to the northeast, east, and southeast. When a solifuge was encountered, fluorescent paint was applied using a fine-tip paintbrush on both the pro- and opisthosoma in a unique combination of colors so that individuals could be recognized if re-captured (Fig. 1C). The geographic coordinates for each encounter were recorded, as was the sex (unless immature), time

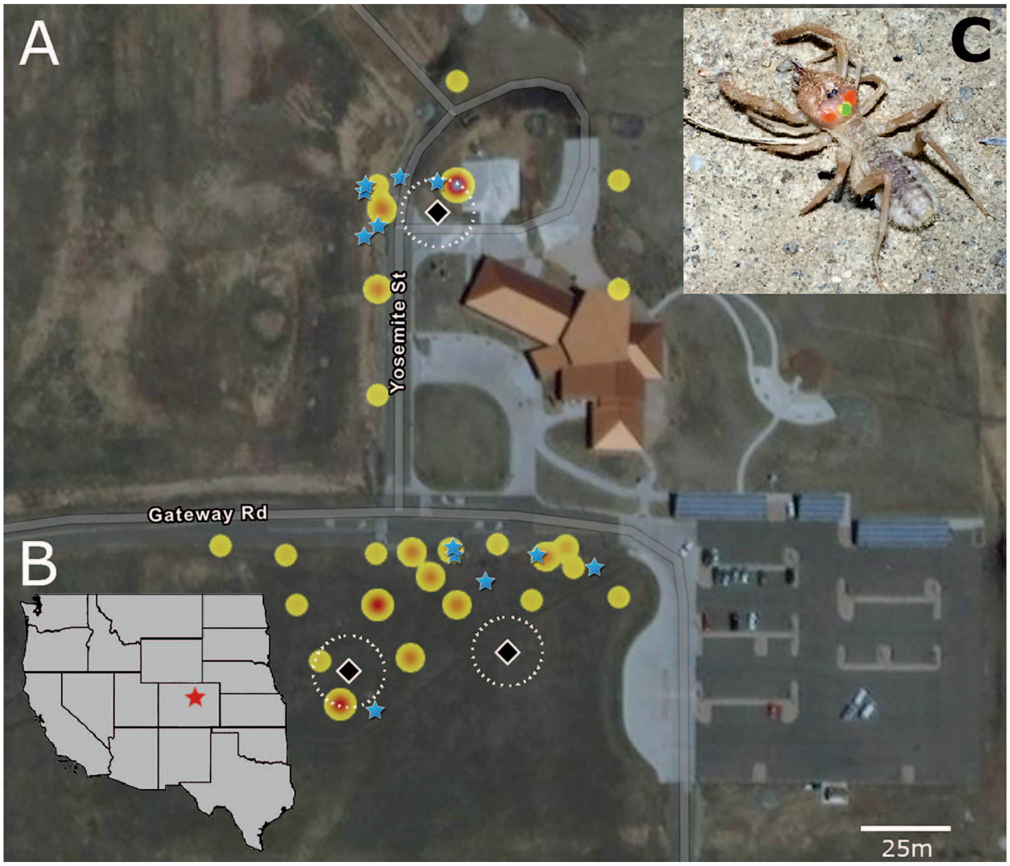

Figure 1.—Aerial image of the study area and example of tagging scheme. (A) Map of visitors' center at Rocky Mountain Arsenal National Wildlife Refuge (RMANWR) with localities of captures (yellow-red heatmap circles), re-captures (blue star), and lanterns (black diamonds). The heatmap circles are reflective of the number of individuals caught per location, ranging from one capture (plain yellow) to four captures (red and blue concentric circles). Dotted white circles indicate a radius of 10m as estimated in ArcGIS software. (B) Map of Western United States, location of RMANWR indicated by the red star. (C) Image of an adult female putative *Eremobates palpisetulosus* with a unique color tag on the prosoma.

of capture, putative species identity, and paint color pattern. Solifuges were then released at the point of the initial encounter. The temperature, windspeed, and relative humidity of Commerce City, Colorado (the nearest municipality) were recorded at the beginning of each collection period (Table 1). As in Gore & Cushing (1980), we initially sought to find and flag burrows by flipping rocks. However, the study area consisted of a completely sandy substrate absent of rocks large enough to provide shelter, precluding a systematic search of burrows and requiring us to rely on serendipitous encounters.

A total of 46 solifuges comprising males, females, and juveniles of *Eremobates pallipes* (Say, 1822), *E. palpisetulosus* Fichter, 1941, and *Eremochelis bilobatus* (Muma, 1951) were caught during the study period (Table 1). Although we cannot make definitive identifications of live animals in the field, we have included putative species identifications based on our experience and taxonomic knowledge of the species distributed in this area (Table 1). Due to the striking morphological dissimilarities between *E. bilobatus* and the two *Eremobates* taxa, we are confident that *E. bilobatus* was only encountered once and was not recaptured. Of the 46 marked solifuges, nine (20%) were recaptured once, and two a second time (Table 1). The geographic distances between initial capture coordinates and recapture coordinates were calculated with R package "geosphere" (Hijmans et al. 2017). On average, recaptures were caught 4.16 m (range = 0.23, 17.21 m) from the previous capture site (Table 1). Over the seven-day period, the average temperature was 24.7°C, with a windspeed of 4.7m/s, and relative humidity of ~34%. Capture rates were low when temperatures were ~2.5°C lower than the average. Three putative burrows were found over the course of the seven days, all of which were in the open, sandy soil. Two of the burrows were found while being actively excavated by an adult female and a juvenile, both burrows angled at < 30° to the surface. The other burrow was constructed near-perpendicular to the surface, situated in a sandy wash, and housed one adult female. It is uncertain if this burrow was constructed by the observed female, or if it was simply occupying one constructed by another solifuge or other burrowing organism. No solifuges were found when the marked burrows were revisited on several occasions (including during daylight), suggesting their use was temporary.

Marked solifuges that were re-encountered in the study area were inferred to exhibit fidelity to the study area. Due to short periods of peak abundance, and the (estimated) one-year life cycle of North American solifuge taxa (Muma 1963, 1966a; Punzo 1998a), year-to-year studies are logistically impossible, while extended study periods within one peak are logistically challenging. In contrast to our findings, Wharton was unable to relocate any of the 75 marked *Metasolpuga picta* (Kraepelin, 1899) in the Namib Desert (Wharton 1987). If solifuges are constantly traveling during and between nightly active periods, and in random (or at least unpredictable) directions, a recapture rate of 20% is surprisingly high. Considering that solifuges are extremely active and can travel hundreds (and over a thousand) meters per hour, we believe all re-captures to be notable (Muma 1967; Cloudsley-Thompson 1977; Wharton 1987; Punzo 1998c). This small study, although limited, suggests that individual *Eremobates* solifuges

Table 1.—Summary of total number of captures and recaptures with putative identifications of recaptures. The range of dates in the "date" column reflects the start of collection at approximately 20:30 on the first date and ending between 01:00 and 01:30 the morning of the second. Of the 46 initial captures, 45 were *Eremobates* and one was a *Eremochelis*. All recaptures are members of the genus *Eremobates*. Superscripts * and ** refer to the first and second recapture of the same individual, respectively, as do superscripts + and ++. $\bar{x}$ indicates the average of the weather variable over the seven-day study period.

Capture Date	# Caught	# Male	# Female	# Immature	Start Temp (°C)	Windspeed (m/s)	Relative Humidity (%)
7/1-7/2	6	4	2	0	26.1	5.8	17
7/2-7/3	6	4	2	0	24.4	3.5	33
7/3-7/4	7	5	2	1	23.9	6.3	38
7/4-7/5	1	1	0	0	22.2	2.2	61
7/5-7/6	2	1	1	0	22.2	4	40
7/6-7/7	18	11	4	3	26.1	5.8	26
7/7-7/8	6	4	2	0	27.7	5.3	24
TOTAL	46	30	14	4	$\bar{x} = 24.7$	$\bar{x} = 4.7$	$\bar{x} = 34.14$

Orig. Cap. Date	Cap. Time	Recap. Date	Recap. Time	Putative Species	Sex	Distance from Orig. Cap. (m)
7/2-7/3	22:40	7/2-7/3	23:24	*E. pallipes*	Male	3.1493079
7/2-7/3	0:40	7/3-7/4	23:07	*E. pallipes*	Male	8.8750784
7/2-7/3	23:53	7/3-7/4	1:05	*E. pallipes*	Male	0.2328035
7/1-7/2	0:03	7/5-7/6	0:45	*E. pallipes*	Male	2.2948179
7/5-7/6	0:24	7/6-7/7	21:48	*E. palpisetulosus*	Female*	2.2187696
7/6-7/7	21:48	7/6-7/7	23:12	*E. palpisetulosus*	Female**	3.3318842
7/6-7/7	21:55	7/6-7/7	23:30	*E. palpisetulosus*	Female+	4.1764289
7/6-7/7	23:20	7/7-7/8	23:19	*Eremobates* sp.	Imm.	1.441378
7/3-7/4	0:50	7/7-7/8	22:15	*E. palpisetulosus*	Female	0.921463
7/3-7/4	23:24	7/7-7/8	23:19	*E. palpisetulosus*	Female	17.2106752
7/6-7/7	23:30	7/7-7/8	0:54	*E. palpisetulosus*	Female++	1.8817286

exhibit philopatric behavior. The use of lights to attract solifuges may have increased our likelihood of encountering focal specimens, however we believe this effect to be minimal based on the data presented here. Only eight of the initial captures and one recapture were within 10 m of a lantern, a distance that well exceeds the observable pool of light generated by the equipment. Additionally, the portable lights used were competing with the light pollution from industrial buildings, sporting centers, and residential housing surrounding RMANWR (closest being <630 m away) and therefore potentially reducing the effectiveness of the portable lights.

It is worth noting that males make up 64% of total marked individuals but only 36% of recaptures, indicating males may be more mobile, as in some other arachnid groups (Polis et al. 1985; Vollrath 1998; Benton 2001; Bond et al. 2001; Hendrixson & Bond 2005; Stoltey & Shillington 2009; Foelix 2011; Buzatto et al. 2013; Peres et al. 2015) and reflective of different maturation times between the sexes. Notably, all recaptured specimens putatively identified as *E. pallipes* were males, while all putative *E. palpisetulosus* recaptures were females. These findings are congruent with Denver Museum of Nature and Science records that indicate abundance of male *E. pallipes* peaks in early July coincidental to the abundance of female *E. palpisetulosus*. The only published data available for North American solifuge life cycles are for *E. durangonus* Roewer, 1934 (Muma 1966c) and *E. marathoni* (Muma, 1951 (Punzo 1998a) in Arizona and Texas, respectively. Both studies indicate that males generally mature and appear a few weeks earlier in the year than females, with male *E. marathoni* abundance peaking in May and *E. durangonus* in July, then rapidly dropping off in the following months, presumably due to mortality (Muma 1966c; Punzo 1998a). This pattern of female abundance peaks in June and July as well but was found to decrease in a steadier pace approaching the fall seasons, presumably during oviposition and brood-rearing (Muma 1966c; Punzo 1998a). These findings are consistent with summarized historical capture data for many North American solifuge taxa (Muma 1974) and our inability to find solifuges, save for one female in four days, when we returned RMANWR in late July and early August to begin another study period.

Additional field investigations that do not involve the use of artificial light sources are needed to form more robust conclusions and develop behavioral and ecological hypotheses. A longer study period encompassing multiple weeks during peak abundance between early-to-mid June and late July would likely increase sample size and facilitate more observations regarding sexually dimorphic behavior. Additionally, this extended study period would lead to increased detection of burrows, and thus increase our ability to monitor burrows over a period of time. Further evidence of site fidelity and burrow re-use would strongly suggest the presence of homing behavior in North American solifuges, and prompt further investigation into navigational mechanisms. Lastly, a well-developed understanding of solifuge behavior regarding site fidelity or home ranges would elucidate dispersal ability, gene flow, and population structure.

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