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SHORT COMMUNICATION

Submersion tolerance in a lakeshore population of *Pardosa lapidicina* (Araneae: Lycosidae)

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Abstract. Terrestrial animals often inhabit stochastic boundaries between terrestrial and aquatic habitats which are under constant risk of flooding. In these circumstances, terrestrial arthropods often exhibit behavioral and physiological adaptations to cope with this risk by either avoiding flooding or tolerating submersion. We present the results of a study designed to explore submersion tolerance in a lakeshore population of *Pardosa lapidicina* (Emerton 1885), a eurytopic lycosid. Spiders were submerged in lake water for 4, 8, 11, or 16 hours, then removed and tested for responsiveness. Each spider was checked for responsiveness a second time after an eight-hour period in a dry vial. Spiders that were submerged for longer periods were less likely to be responsive immediately after removal. However, between 7% and 38% additional spiders resumed activity eight hours after removal, their recovery depending on their time submerged. This suggests that adult *P. lapidicina* can survive long periods of submersion in a quiescent state and later resume activity.

Keywords: Eurytopic lycosid, habitat flooding, stone spider

The marine intertidal, lakeshore, tidal marsh and riparian zones are inundated by recurrent though often irregular flooding, and terrestrial organisms living in these habitats must contend with abiotic stressors associated with the nearby water edge (Helmuth & Hofmann 2001; Plum 2005). Organisms that exhibit the traits necessary to successfully utilize this habitat are presented with novel and abundant resources (Leigh et al. 1987; Paetzold et al. 2008). Furthermore, many actively foraging terrestrial organisms opportunistically utilize these habitats only when conditions are favorable (e.g., low tide, dry seasons).

The onset of flooding (e.g., tidal flux, rainfall, waves) can elicit short-term horizontal dispersal to dry habitats or vertical dispersal to dry vegetation or rocks (Morse 1997; Adis & Junk 2002). Seasonally, terrestrial arthropods often migrate as a result of ephemeral flooding such as advancing wetted fronts in dry riverbeds (Corti & Datry 2012). Nevertheless, for animals that live near the water's edge without access to aerial refugia, rapid flooding may present an unpredictable danger of drowning. Animals may reduce this risk behaviorally by finding refuge under shells, in crevices or nests, or in bubbles created by rock asperities (Rovner 1986; Maitland & Maitland 1994). In addition, physiological adaptations (e.g., submersion tolerance) may accompany these behavioral traits, especially in stenotopic arthropods living in salt-marshes and along lakeshores and riverbeds (Foster & Treherne 1976; Witteveen & Joosse 1988; Decleer 2003; Rothenbücher & Schaefer 2006). For example, the salt-marsh lycosid *Arctosa fulvolineata* (Lucas 1846) has been shown to enter a state of hypoxic coma when submerged in salt water for extended periods of time (Pétillon et al. 2009). Spiders that undergo hypoxic coma become unresponsive to external stimuli, though they are able to resume activity eight hours after removal from the water (Pétillon et al. 2009).

Despite a few studies on behavioral responses to flooding, submersion tolerance has not yet been tested in a lakeshore population of a eurytopic lycosid. *Pardosa lapidicina* (Emerton 1885) is a wolf spider which inhabits rocky habitats, from talus slopes to rocky shorelines (Eason 1969; Bradley 2012). Some populations of *P. lapidicina* have been shown to migrate back and forth along the marine intertidal, following the tides (Morse 1997), allowing them to take advantage of novel foraging opportunities (Morse 2002). Many *Pardosa* species have been shown to exhibit rapid locomotion along water surfaces via a characteristic rowing behavior (Stratton et al. 2004). However, if a spider is caught under a rock or in an exposed crevice during high tide, under a wave, or during a flash flood, locomotor responses may be insufficient to save it from drowning. The ability to withstand drowning may be especially important for populations near bodies of water with unpredictable changes in surface level. This could occur along the shores of the Great Lakes in areas that experience heavy boating activity and seiches (i.e., standing waves occurring in enclosed bodies of water produced by atmospheric disturbances and storms) (Gedney & Lick 1972; Herdendorf 1987). Gibraltar Island on Lake Erie is home to a population of *P. lapidicina* whose range, at least for part of the year, is limited to a few small rocky shorelines that experience drastic and sudden changes in wave size and water level (*pers. observation*). How might individuals cope with sudden inundation and what would be the survival consequences. In this paper, we address two questions: (1) Will individual *P. lapidicina* be responsive after submersion for extended periods? and (2) Will initially unresponsive individuals later resume activity?

Adult *P. lapidicina* (n = 43) were collected from two small rocky lakeshores along the eastern side of Gibraltar Island in the Bass Island region of Lake Erie. Experimentation took place during June 2013 when both adult males and females were present, one day after a mayfly emergence and the day before a storm with wind gusts up to 17 m/s (NOAA National Data Buoy Center). Under these conditions, spiders had likely fed *ad libitum* in the field, and were collected one day prior to a weather event that could have produced our experimental conditions *in situ*. After 24 hours in captivity, the mass of each spider was measured on a digital scale. Spiders were then submerged individually in vials filled with freshly collected lake water and the vials were submerged in a large container to standardize ambient water temperature (18.7°C–18.8°C over the course of the experiment). Care was taken to ensure that all air bubbles were expelled from the vials. Spiders of both sexes were randomly assigned to groups that would be submerged for 4, 8, 11, or 16 hours. The resulting groups were composed as follows: 4 hours: 6 female, 3 males; 8 hours: 6 females, 2 males; 11 hours: 12 females, 2 males; 16 hours: 6 females, 5 males). At the end of submersion, each spider was individually placed under a dissecting microscope, ventral side up. After a 30 second acclimation period, the ventral abdomen was stroked with a fine paintbrush every 5 seconds for three minutes. The proportion of individuals that resumed activity after submersion was recorded for each submersion duration. Individuals were then placed in dry vials and allowed 8 hours to recover from the submersion, at

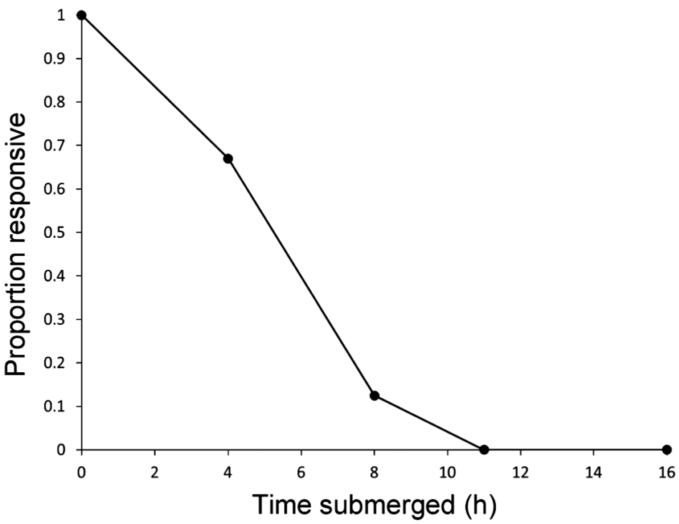

Figure 1.—The proportion of spiders responsive to tactile stimuli after removal from the water decreased the longer they were submerged (χ^2_3 = 19.8, p = 0.0002).

which point they were re-tested for responses to tactile stimulation. Voucher specimens were placed in the Spider Biology teaching collection at Stone Laboratory and the Pruitt Lab at the University of Pittsburgh. Data were analyzed with two nominal logistic regressions with time submerged, sex, and body mass (g) as independent variables and one of two nominal dependent variables: (i) responsiveness of individuals immediately after removal from the water and (ii) resumption of activity 8 hours after removal.

Spiders that spent more time submerged were less likely to be responsive to tactile stimulus immediately after removal from the water (χ^2_3 = 19.8, p = 0.0002; Fig. 1). This trend did not differ between sexes (χ^2_1 = 0.74, p = 0.39) and was not influenced by body mass (χ^2_1 = 0.04, p = 0.84). However, some spiders were active 8 hours after the end of submersion even though they had been unresponsive immediately after submersion, and that recovery was influenced by time submerged (χ^2_1 = 22.9, $p < 0.0001$; Fig. 2). All spiders that were responsive immediately and 8 hours later remained alive and ambulatory in captivity for 48 hours after experimentation. This suggests that, in the case that an adult spider is inundated by rising water level, it may survive up to 11 hours of submersion in a quiescent state, and later resume activity.

It is unknown if this observation is the result of physiological adaptations like hypoxic coma (Pétillon et al. 2009) or anatomical artifacts such as patterns of setae which capture extra air bubble volume as in the diving bell spider and other diverse spider families (Suter et al. 2004; Seymour & Hetz 2011). It is surprising that body mass did not play a role in survivorship, as body size can be pivotal in the success of attached bubbles as physical gills for terrestrial arthropods (Anderson & Prestwich 1982; Seymour & Matthews 2013). It may be that the spiders used in this study did not vary enough in body mass within each sex (females: 0.07 ± 0.03g; males: 0.03 ± 0.006g) to allow detection of an effect of body mass on survivorship. Furthermore, tradeoffs between larger body size and surface:volume ratio could mask many differences between large and small individuals (e.g., Tufová & Tuf 2005). In order to fully understand resistance to drowning in lycosids, comprehensive studies should simultaneously test the relationship between flood avoiding behavior (e.g., Stratton et al. 2004; Lambeets et al. 2008), physiological submersion tolerance (Pétillon et al. 2009) and hydrophobic anatomical characters (Stratton et al. 2004; Seymour & Hetz 2011). Comprehensive studies exist on behaviors like water surface locomotion in terrestrial spiders (Stratton et al. 2004) from

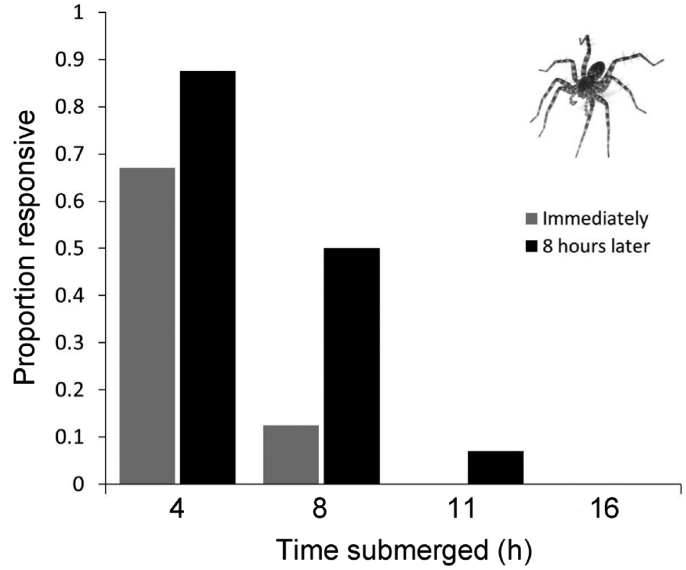

Figure 2.—More spiders were responsive 8 hours after removal than were immediately after removal, and submergence time drove this trend (χ^2_1 = 22.9, $p < 0.0001$). No spiders which had been submerged for 16 hours were responsive immediately after removal or 8 hours later. Photo by Tom Adams.

which information can be derived to further understand the strategies employed by different species before and after submersion. Furthermore, studies across life stages may address life history tradeoffs and stage-dependent strategies. For example, during the collection period, many female spiders were observed carrying egg cases. It is unknown how submersion affects *P. lapidicina* eggs, though submersion tolerance has been observed in the egg stage of two *Allomengea* spp. Strand (Araneae: Linyphiidae) (Rothenbücher & Schaefer 2006). The propensity to evade flooding conditions may be experiential, an artifact of habitat specialization and/or plenotypic plasticity, or a product of adaptation (Morse 2002; Lambeets et al. 2008, 2010).

Subsequent studies which test spiders across habitats may also broaden our understanding of local adaptation within populations across variable habitats very near one another. Lycosids along small inland ponds have been shown to migrate very little over time, suggesting that habitat retention may be adaptive in habitats with reliably stable water edges (Ahrens & Kraus 2006). Lastly, detailed studies across sites with varying anthropogenic activity will illuminate the influence of human-induced rapid environmental change (Sih et al. 2011; e.g., the production of boat wakes and the introduction of invasive salt-marsh grasses; Pétillon et al. 2010) on the emergence, persistence, or loss of behavioral and physiological defenses against habitat flooding.

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