

# Aggregation and site tenacity under downed logs in *Salamandrella keyserlingii* (Caudata: Hynobiidae)

Masato Hasumi · Tsagaan Hongorzul ·  
Masahiro Nakagawa

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**Abstract** Darhadyn Wetland, Mongolia, is located in a subarctic steppe–tundra climate, where salamanders are exposed to both extremely hot and cold environments. We hypothesized that log refugia provide an adaptive advantage to salamanders in these environments because the habitat availability hypothesis predicts that restricted habitat availability can cause aggregation that plays a role in the initial stages of the evolution of complex sociality. To test this hypothesis, we assessed whether a rare salamander species aggregated under a limited shelter resource. Many small vertebrates use terrestrial burrow refuges. While many salamander species also use burrows, *Salamandrella keyserlingii* at Darhadyn used only downed log refuges (i.e., restricted habitat availability). Some individuals displayed site tenacity to remain under a specific log, and one or more of the same individuals were located continually or frequently under the same logs. The majority of recapture events (96.8 %, 121/125) did not show any movements of salamanders between logs. Of the 300 capture events, 66 % were aggregating. The maximum number of individuals

sharing a log refuge on the same day (i.e., sharing group size) ranged from 2 to 9. Individuals were resident non-randomly in downed log refuges, i.e., an aggregation pattern was nonrandom. Based on these findings, we provided conservation measures such that total number of individuals captured per log over the course of the study (maximum number = 32) had a positive relationship to 1 of 7 explanatory variables (i.e., log decaying class in ascending order). Thus, the retention of decaying downed logs is important for the conservation of this species.

**Keywords** Evolution of complex sociality · Habitat availability hypothesis · Microhabitat use · Spatial ecology · Subarctic climate · Terrestrial refuge

## Introduction

The habitat availability hypothesis relies on the fact that refuges from unfavorable situations such as predation, climate change, and fire are restricted in ecological settings (Heino and Soininen 2006; Hill et al. 2006; Pike et al. 2011). If a species' microhabitat is limited to only one type of refuge, the species may “aggregate” (defined as the clustering of individuals within a given sex or age class over small intervals of distance: e.g., Loher and Hobden 2012) within that refuge. That is, the habitat availability hypothesis predicts that with limited availability of suitable refugia, animals should use a single space for an extended period of time, and the space should be shared among conspecifics (Bulova 1994; Chapple 2003). Such aggregation can play a role in the initial stages of the evolution of “complex sociality” (defined as stable aggregation: e.g., Chapple 2003).

Considerable numbers of small animals use various terrestrial refuges such as burrows, downed logs, woody

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M. Hasumi (✉)  
Biological Institute, Faculty of Science, Niigata University,  
Niigata 950-2181, Japan  
e-mail: mhasumi@bio.sc.niigata-u.ac.jp

T. Hongorzul  
Department of Biology, Mongolian State University of  
Education, Ulaanbaatar 210648, Mongolia

M. Nakagawa  
Department of Fisheries, Faculty of Agriculture, Kinki  
University, Nara 631-8505, Japan

*Present Address:*  
M. Nakagawa  
Wetland International Japan, Chuo-ku, Tokyo 103-0013, Japan

debris, leaf litter, moss mats, crevices, and rocks (Sherwood et al. 2012). Among these refuges, burrows provide refuge from predation and nesting to increase mating opportunity for many small vertebrates, including mammals such as prairie dogs and rodents (Roper et al. 2002; Ebensperger and Blumstein 2006), avian species such as parrots and trogons (Brightsmith 2005), and reptiles such as desert tortoises and lizards (Chapple 2003; Harless et al. 2009). Burrows also function to reduce desiccation and heat in amphibians during daytime in summer (Hasumi et al. 2009). In addition to the use of burrow refuges, many small vertebrates use downed logs (or at least coarse woody debris, which is similar to logs) with approximately the same or lower frequency (e.g., Anthony et al. 1997; Toll et al. 2000; Marsh and Goicochea 2003). In these small animals, the aforementioned restricted habitat availability may also cause site tenacity.

The term “site tenacity” as a component of territoriality is defined as a persistent attachment of individuals to a specific location (e.g., Chapple 2003) and has been explored for numerous aquatic and terrestrial animals (e.g., Ousterhout and Liebgold 2010; Thaker et al. 2010). The concept of site tenacity for refuge would fit with representation of how animals survive at extreme environments if habitat availability is limited. Thus, small animals are exposed to potential habitat threats. For example, in recent decades, nomadic humans in Mongolia and an adjacent area of China have resided in houses made of downed logs (Aassve and Gereltuya 2002; Zhang et al. 2007). This cultural change in nomads may be reducing the availability of downed logs as terrestrial refuges for small animals. That is, nomadic collection of downed logs can influence the animals’ site tenacity to downed logs. Also, climate change by the progress of global warming may melt the permafrost, resulting in unsuitable log refuges exposed to high temperatures. However, site tenacity to downed logs has not widely been reported in vertebrate taxa other than mammals (Michael et al. 2004). For example, 98 % of the collective locations of voles are associated with downed logs although their association is not always repetitive in the same logs, some data of which indicate multiple observations at one location (Tallmon and Mills 1994). If a similar site tenacity or association to downed logs is observed in amphibians that use various refuges, this would thus cause aggregation beneath the logs.

In this context, specific research questions were as follows. (1) Are logs shared by multiple individuals? (2) Do these individuals show levels of tenacity toward a particular refuge? To address these questions, we collected data on refuge use by salamanders at a unique population that uses only downed logs as refuges. Based on these results, we discuss the potential consequences of aggregation for this species. Our second goal was to determine physical

parameters of downed logs that were used for refuge and sometimes shared among multiple salamanders, focusing on associations with the permafrost region affected by global warming and sandy desertification (Hasumi et al. 2007; Zhang et al. 2007), and to provide fundamental knowledge for conservation measures of log-associated amphibians.

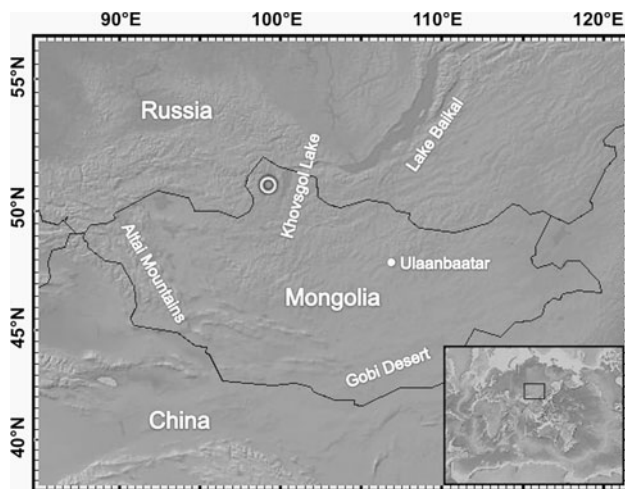
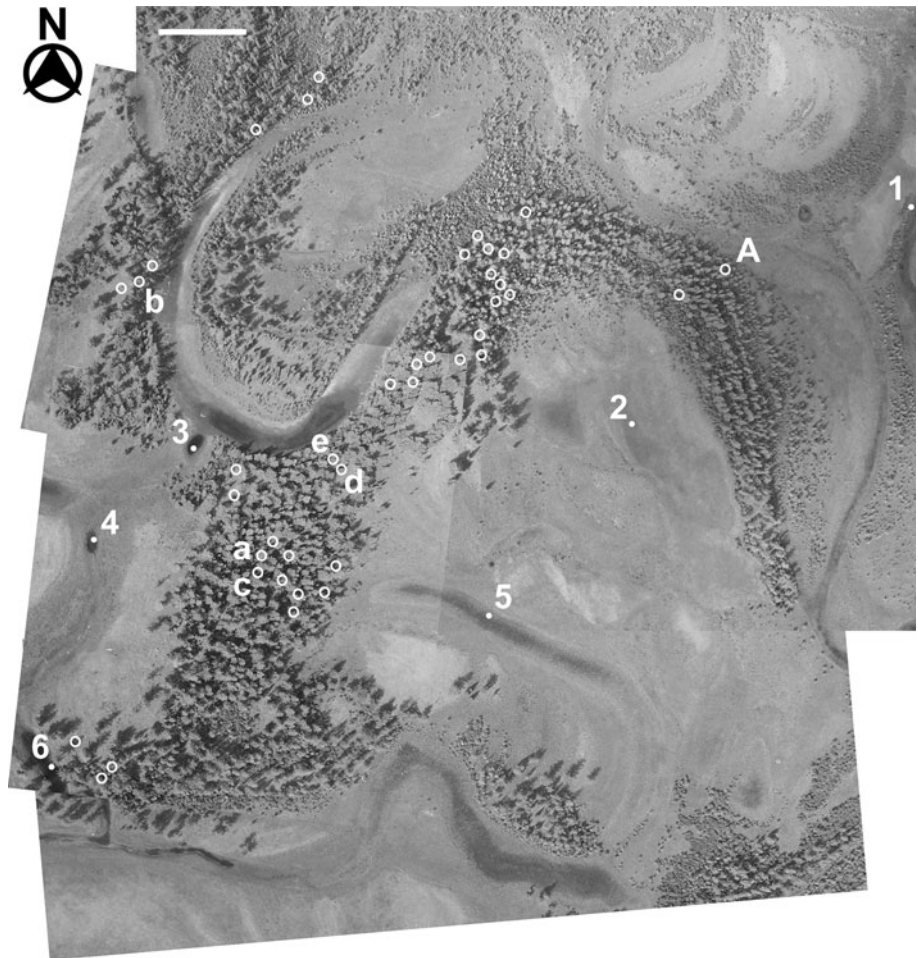
## Materials and methods

### Study animal and area

*Salamandrella keyserlingii* Dybowski, 1870 is a member of the primitive extant salamander family Hynobiidae (Amphibia: Caudata) and has the broadest range of any amphibian species worldwide (~12 million km<sup>2</sup> from 43 to 72°N), extending from eastern Europe through subarctic Siberia to Kamchatka Peninsula and Kurile Islands, including the northern portions of Kazakhstan, Mongolia, China, North Korea, and Japan (Borkin 1999). This species is not rare in Russian areas, which correspond to most of the species’ distributions, but is endangered in Mongolia (Shiirevdamba 1997). We conducted this study at a 20-ha forested zone (50°58’N, 99°25’E; 1,560 m elevation) comprised of a single conifer species (*Larix sibirica*), several off-channel oxbow lakes, ephemeral and permanent pools, sedge meadows, and discontinuous grassland within a wetland complex in a floodplain (Fig. 1). The floodplain is associated with the Shishkhid River (40–60 m wide), winding through the southern part of Darhadyn Wetland (Fig. 2). This wetland is widespread in Tsagaan Nuur, the western side of the Khovsgol Lake, Khovsgol Province, Mongolia (130 × 30 km area; 50°40’–51°40’N, 99°15’–99°45’E; 1,540–1,580 m elevation; mean yearly air temperature was –8.31 °C: Hasumi and Borkin 2012; sunset occurred between 2130 and 2300 hours in July–August: for a satellite picture see Hasumi et al. 2007). Due to a subarctic steppe–tundra climate (Köppen climate classification: Dwc), no broad-leaved trees were found within the study area. Melting of the frozen soil around early June led to poor road conditions and hindered access to the study area, i.e., monitoring at times of the year other than summer was not easy. At Darhadyn, *S. keyserlingii* was the one and only amphibian species (Hasumi et al. 2007).

From August 23 to 24, 2002, and from July 25 to 26, 2003, the second author and her colleagues scoured all the study area of 20 ha for available refuges such as small burrows, cracks, and crevices and decided that the only possible refuge for *S. keyserlingii* was under downed logs (=restricted habitat availability). In this area, there were no rocks to hide under and no crevices around tree roots or no leaf litter (due to the absence of broad-leaved trees), in

**Fig. 1** Aerial view of the 20-ha study area with discontinuous forested zones of a single conifer species (*Larix sibirica*), containing several off-channel crescent lakes and pools (photographed by T. Morita from a motor paraglider). Locations of 40 downed logs were indicated by *open circles* (site A = initial point for daily surveys); and aquatic trapping sites 1–6, by numbers. Salamander larvae were captured from sites 2, 4, and 5, where no fish were captured. Sites a–e were given for the examples of aggregation and site tenacity (see Table 3). Scale = 50 m



**Fig. 2** Small-scale topographic map showing the location of our study site (Darhadyn Wetland, Tsagaan Nuur, Khovsgol Province, Mongolia: 50°58'N, 99°25'E; 1,560 m elevation: denoted by an *open circle*), featuring a large-scale outline map to indicate the regional context of our study site in the world (*lower right corner*: a *small rectangle* within a *large rectangle* represents the location of the small-scale map)

which salamanders could hide. Further, while less than 10 mammalian burrows were found, burrow use by salamanders was not observed. On July 18, 2004, and from August 6 to 7, 2005, we confirmed the results of their search for refuges, i.e., six observers including us searched for available refuges again in this area simultaneously during our log assignment and re-identification over 30 h. Having downed logs as the only available refuge provided a rational, feasible context for testing the habitat availability hypothesis. In comparison, proportional refuge use by *S. keyserlingii* at Shaamar, Mongolia, is 0.707 for burrows and 0.185 for downed logs (Hasumi et al. 2009).

#### Monitoring techniques

We found ca. 60 logs scattered over the study area in 2004. These logs were derived from naturally fallen trees. Because we did not find any newly downed logs in 2005, there were no potential effects of logging practices such as those by resident nomads on spatial behavior of salamanders. Logs were not lost to decay between years, and the

refuges observed were exactly the same in 2004 and 2005 (i.e., no effect on log decaying classes).

On July 18, 2004, we randomly selected 40 of the 60 identified logs to use in the study, limiting ourselves to 40 logs due to animal processing time and remoteness of our study area from a campsite (Fig. 1). We began our daily surveys at the same initial point of the site A and detected salamanders by the same route. We assigned those logs a number using a hand tacker and number tapes, after which we mapped the whole region associated with assigned logs. We used a “global positioning system” (GPS: at least eight satellites, to within 8 m) to determine the location of downed logs occupied by individual salamanders. There were only six pools seemingly available for breeding of *S. keyserlingii* within the study area (for details see below), while this species also might breed in other nearby locations in the wetland complex. We measured distance of each log from the edge of a nearest pool, as well as size (length and diameter at a central appearance) of each log. We categorized the 40 logs into four decaying classes in ascending order on July 20, 2004, by a modification of Lienkaemper and Swanson’s (1987) degree of woody debris: (1) bark adhering tightly to hard core, (2) loose bark and hard core, (3) loose bark and soft core, and (4) no bark and soft core.

From August 6 to 7, 2005, we re-identified 39 of the original 40 logs, by referring to the previous log data and photographs, because their number tapes were lost due to the incidental collection by resident nomads (one still had the number tape attached). We mapped the location of each log on aerial photographs, taken from a motor paraglider in 2004 (Fig. 1). We incorporated the information from 2004 about the presence or absence of *S. keyserlingii* larvae and fish predators in each pool (see “Aquatic larvae”) and again measured the distances from logs to nearest pools that contained salamander larvae but did not contain any fish predators (hereafter “fishless pools”) using a GPS and a measuring tape. This measurement was conducted to quantify distance that “metamorphs” (defined as individuals that completed metamorphosis within the last month) had to travel in order to find suitable terrestrial refugia.

We conducted daily surveys from July 19 to 23, 2004, except 20 July when heavy rain prevented a survey (4-day survey) and from August 8 to 17, 2005 (10-day survey). We measured physical parameters around the 40 logs: temperature and relative humidity in the ambient air 1.5 m above the log and under the log (by looking for gaps in the soil; averaged by random three-point measurements) with a thermo-hygrometer (SK-110TRH, Type 2: Sato Keiryoki Mfg. Co., Ltd., Tokyo, Japan); illumination intensity on and under the logs (at a gap in the soil) with a light meter [LX-100 (sensitivity: 0–1,999 lx = 1 lx; 2,000–19,990 lx = 10 lx): Fuso Co., Ltd., Tokyo, Japan]; and soil pH beneath the log

(averaged by random three-point measurements) with a compact, portable pH meter (Twin pH, B-212: Horiba Ltd., Kyoto, Japan) calibrated before measurement with pH 7 and pH 4 standard solutions. We placed the soil in a sensor box of the pH meter and immersed it with distilled water before measuring pH. We regarded 19,990 lx or more illumination intensity as 19,990 lx (technical limit of the instrument). We did not collect data on illumination intensity in 2004 because of the absence of a light meter, and lack of relative humidity data in 2004 was due to heavy rain that broke the hygrometer sensor. After measuring the physical parameters, we searched for salamanders hidden under the log by turning it over. Immediately after finding an individual, we caught the salamander by hand and kept it temporarily in a cooler box with divided areas (to distinguish each individual prior to marking) and moist sphagnum moss (to prevent desiccation).

We recorded age class, sex, and visual characteristics such as throat coloration and dorsal color pattern of each individual (Hasumi 2001b). We weighed each individual to within 0.05 g using a beam balance and measured the broadest head width, maximum tail height, snout–vent length (SVL: distance from the tip of the snout to the posterior angle of the vent), and tail length (from the posterior angle of the vent to the tip of the tail) to within 0.01 mm using digital calipers by a modification of Wise and Buchanan’s (1992) method without using anesthesia. Based on these measurements, we categorized all individuals into five classes (for size classes, see Table 1): adult males, adult females, unsexed individuals, juveniles (over one year old), and metamorphs (less than one year old). Males were identified as those with a pale-yellow throat, a “secondary sexual characteristic” (SSC) that appears late in the breeding season and only occasionally lasts into the summer (Hasumi 2001b). Females were identified as those with a beige ovisac (i.e., homologous uterus) visible through the skin of the ventral region of the torso near the hindlimbs, despite earlier reports that ovisacs are visible only in fall–spring (Hasumi 1996). The remnant of SSCs in both sexes indicated that at Darhadyn, summer came shortly after breeding activity ceased. We defined unsexed individuals as those without SSCs but with larger body size than the smallest adult female (45.93 mm SVL). We chose this female’s size as a threshold for the smallest unsexed individual because female-larger sexual size dimorphism was evident. Because of difficulty in distinguishing metamorphs from juveniles by body size, we used for the distinction skeletochronological analyses based on toe clips (Hasumi and Borkin 2012).

We individually marked large- and medium-sized salamanders ( $\geq 40$  mm SVL) with a “passive integrated transponder” (PIT) tag (13 × 2 mm microchip, standardized by ISO: Datamars, Bedano, Switzerland) by injecting it intraperitoneally. We marked small-sized salamanders

**Table 1** Mean number of times salamanders were found under logs, and body size (SVL snout–vent length) of salamanders for each sex or age class

| Sex or age class                    | <i>N</i> | Number of times<br>Mean ± SE (range) | <i>N</i> | SVL (mm)<br>Mean ± SD (range) |
|-------------------------------------|----------|--------------------------------------|----------|-------------------------------|
| Adult males                         | 32       | 1.78 ± 0.36 (1–7)                    | 18       | 53.08 ± 4.05 (46.02–59.38)    |
| Adult females                       | 28       | 1.65 ± 0.24 (1–4)                    | 15       | 59.05 ± 7.59 (45.93–73.39)    |
| Unsexed individuals                 | 59       | 1.97 ± 0.32 (1–8)                    | 29       | 48.67 ± 2.14 (45.93–53.28)    |
| Juveniles (over one year old)       | 77       | 1.79 ± 0.24 (1–8)                    | 43       | 39.61 ± 3.17 (35.03–45.26)    |
| Metamorphs (less than one year old) | 104      | 1.48 ± 0.11 (1–6)                    | 70       | 32.15 ± 2.99 (21.36–38.09)    |

SVL data were recorded only on first capture to ensure their independency ( $N = 175$ )

including metamorphs (<40 mm SVL) with up to one toe clip per appendage (i.e., nonadditive toe clips). Although it was unknown whether the tags or toe clipping had some adverse effect on these salamanders (such as renouncing favorable refuges), their recapture rates (see “Capture–mark–recapture”) were higher than those of other salamander species such as *Plethodon kentucki* (Marvin 2001) and *Ambystoma maculatum* (Blackwell et al. 2003), suggesting little adverse effect. This is most likely because a short intercapture interval sufficiently prohibits site tenacity of individual salamanders (Monti et al. 2000; Marsh and Goicochea 2003; Bailey et al. 2004), and our intercapture interval was only 1 day irrespective of high recapture rates. We released marked salamanders at the site of capture within the log and attempted to reconstruct the log. We identified marked salamanders by reading an intraperitoneal PIT tag with a tag reader or by reading a unique combination of the toe clips. After the first time salamanders were captured within a year, we did not measure body size characteristics of recaptured salamanders. If recaptured salamanders moved from the original log to another log, we determined distance between these logs.

To identify and characterize aquatic-breeding habitats of salamanders, we set 12 collapsible nylon mesh traps [50 cm long, 5-cm opening in each side for trapping, and 2-mm mesh (size threshold of the sampling protocol): Adams et al. 1997] at the shore in sites 1–6 (two traps per site) on July 19, 2004, and August 7, 2005. The openings of the unbaited traps were at water depths of 20–30 cm, except for the site 2 (water depth <20 cm). We conducted daily trap surveys between 1000 and 1200 hours for 4 days (2004) and 10 days (2005). We used data on larvae and metamorphosis to interpret the unusual abundance of metamorphs during early summer and to know aquatic-breeding locations (=fishless pools). To estimate the onset of breeding activity for *S. keyserlingii*, we went to the study area on May 13, 2006, and investigated the presence or absence of deposited egg sacs in sites 1–6. We realized that the data did not come from the same year, but the remoteness of Darhadyn from Japan and the limited means

of traffic (e.g., horse riding is the only means of traffic during melting of the frozen soil around early June) did not permit more frequent trips.

### Statistical analysis

We performed statistical analyses using the software R 2.15.3 (R Core Team 2013) with all significance levels tested at  $\alpha = 0.05$  (two-tailed). We compared mean number of times salamanders were found under logs among “sex/age classes” (i.e., males, females, unsexed individuals, juveniles, and metamorphs) using the Kruskal–Wallis rank sum test. We tested whether a residency of individuals beneath a log (i.e., aggregation pattern) was random or not using a Chi-squared test. We averaged multiple measures per log to avoid pseudo-replication and then compared: (1) mean temperature between in the air and under the log, (2) mean relative humidity between in the air and under the log, and (3) mean illumination intensity between on and under the logs with the Wilcoxon signed-rank test. We did not combine the data for 2004 and 2005 because of the different duration and month of survey or the different number of parameters examined. We used two generalized log-linear models (Poisson regression and negative binomial regression models) per year of data to explore a relationship between a Poisson- or negative binomial-distributed response variable (i.e., total number of individuals captured per log over the course of the study) and seven explanatory variables (i.e., log length, log diameter, log decaying class in ascending order, mean under-log temperature, mean under-log relative humidity, mean under-log illumination intensity, and mean under-log soil pH). We tested overdispersion of each model with an equation, residual deviance/degrees of freedom ( $df$ ), and a dispersion parameter ( $dp$ ). We then adopted a model selection approach based on Akaike’s information criterion with bias correction ( $AIC_c$ ) and selected a single best-fit model with the lowest  $AIC_c$ . We calculated regression coefficient ( $R^2$ ) of determination for the selected model with an equation, (null deviance – residual deviance)/null deviance. We

could not estimate population size because 122 of 125 recapture data were obtained within a short period (i.e., 4- and 10-day sampling periods in 2004 and 2005, respectively). Results from the sample mean were expressed by mean  $\pm$  SE.

## Results

### Log characteristics

Distance from logs to the edge of nearest pools was  $65.04 \pm 43.00$  m (mean  $\pm$  SD,  $N_{\text{logs}} = 40$ , range 2.0–137.6), but distance to the edge of fishless pools was  $164.34 \pm 78.18$  m (range 76.8–337.8). Length, diameter, and area of logs were  $4.86 \pm 2.66$  m (range 0.84–12.10),  $0.30 \pm 0.10$  m (range 0.14–0.60), and  $1.49 \pm 1.04$  m<sup>2</sup> (range 0.18–4.84), respectively. When analyzing data on all capture events, including those of single salamanders without aggregation, mean number of times individuals were found beneath logs did not differ among sex/age classes (Kruskal–Wallis  $\chi^2 = 1.592$ ,  $df = 4$ ,  $P = 0.8102$ ; Table 1). This occurred despite a difference in SVL of each sex or age class [other body size parameters are shown in Hasumi and Borkin (2012)].

For 4-day survey in 2004, negative binomial regression was fitted best [overdispersion = 3.163 (Poisson:  $dp = 1$ )  $> 1.393$  (negative binomial:  $dp = 1.665$ ); minimum  $AIC_c = 178.80$  (Poisson)  $> 137.62$  (negative binomial)] but had no relationship between total number of individuals captured per log (range 0–13) and five measured variables (log length, log diameter, log decaying class in ascending order, mean under-log temperature, and mean under-log soil pH). For 10-day survey in 2005, negative binomial regression was also fitted best [overdispersion = 3.232 (Poisson:  $dp = 1$ )  $> 0.865$  (negative binomial:  $dp = 0.747$ ); minimum  $AIC_c = 233.12$  (Poisson)  $> 206.64$  (negative binomial)], and a positive relationship was found between total number of individuals captured per log ( $y$ -axis: range 0–32) and log decaying class in ascending order ( $x$ -axis:  $y = \exp(0.874x - 0.738)$ ;  $N_{\text{individuals}} = 239$ ,  $N_{\text{logs}} = 40$ ,  $R^2 = 0.445$ ,  $P < 0.0001$ ) of seven explanatory variables (log length, log diameter, log decaying class in ascending order, mean under-log temperature, mean under-log relative humidity, mean under-log illumination intensity, and mean under-log soil pH).

### Physical parameters

Weather conditions were much the same between July 2004 and August 2005. When multiple measures were averaged per log ( $N_{\text{logs}} = 40$ ), temperature was lower under the log than in the air in July 2004 (air:

mean  $\pm$  SD =  $17.46 \pm 2.42$  °C, range 12.30–23.50; log:  $10.13 \pm 2.28$  °C, range 4.99–14.95; Wilcoxon  $V = 820$ ,  $P < 0.0001$ ) and August 2005 [air:  $16.09 \pm 0.96$  °C, range 13.68–17.99 (unaveraged maximum = 33.3 °C recorded on 8 August); log:  $10.65 \pm 1.27$  °C, range 7.81–13.65; Wilcoxon  $V = 820$ ,  $P < 0.0001$ ]. In 2005, relative humidity was greater under the log than in the air (air:  $42.51 \pm 4.64$  %, range 29.90–52.43; log:  $46.72 \pm 8.36$  %, range 31.90–63.41; Wilcoxon  $V = 206$ ,  $P = 0.0053$ ), and illumination intensity did not overlap between in the air and under the log (air:  $12,194 \pm 3,428$  lx, range 5,402–18,164; log:  $4.2 \pm 2.4$  lx, range 1.6–12.8; Wilcoxon  $V = 820$ ,  $P < 0.0001$ ). In 2004–2005, soil pH beneath the log indicated alkalinity ( $8.60 \pm 0.11$ , range 8.37–8.79).

### Capture–mark–recapture

In 2004–2005, there were 300 capture events under 40 downed logs. The number of individuals captured per day ranged from 9 to 46. Several spaces such as gaps in the soil and root tunnels were found along each downed log up to 12 m long, but beneath the log there were no vertebrate and invertebrate tunnels other than those of ants. When we found multiple individuals under a single log, they were aggregated and clumped in one of those spaces and were physically close to each other.

For 4-day survey in 2004, 40 individuals (2 males, 8 females, 14 unsexed individuals, 8 juveniles, and 8 metamorphs) were marked and released, and there were 21 recapture events in 2004 (total capture events = 61; Table 2). For 10-day survey in 2005, 135 individuals (16 males, 7 females, 16 unsexed individuals, 34 juveniles, and 62 metamorphs) were marked and released, and there were 104 recapture events in 2005 (total = 239), including three recapture events from three different individuals marked in 2004. Of two individuals captured eight times from the same log, one unsexed individual was captured daily from the first day to the eighth day, and one juvenile was captured daily from the first day to the seventh day and then was captured again on the tenth day (Table 3, site a). The 62 metamorphs represented 45.9 % of all individuals marked in 2005 (see “Aquatic larvae”). Between 2004 and 2005, we were unable to sex 29 individuals because these salamanders did not retain SSCs during the terrestrial-nonbreeding season when we conducted our sampling.

Among the 2005 recaptures, one female (captured three times) moved from her original log, where she was captured on consecutive days, to a second log 1.7 m distant from her original log when recaptured 2 days later (Movement 1); and one female (captured four times) moved from her original log on the first day to a second log with 1.7 m distance on the second day (Movement 2), returned to her original log on the third day (Movement 3),

**Table 2** Number of salamanders captured once or multiple times (up to eight times) under the same log during daytime in summer 2004 (4-day survey) and 2005 (10-day survey)

| Year | Number of captures |    |    |   |   |   |   |   | Sum |
|------|--------------------|----|----|---|---|---|---|---|-----|
|      | 1                  | 2  | 3  | 4 | 5 | 6 | 7 | 8 |     |
| 2004 | 25                 | 10 | 4  | 1 | – | – | – | – | 61  |
| 2005 | 94                 | 24 | 12 | 2 | 2 | 1 | 3 | 2 | 239 |

and was recaptured under her original log on the fifth day (Table 3, sites d and e). Of the 40 individuals marked in July 2004, three were recaptured from the same or neighboring logs during August 2005: one female and one unsexed individual were found under their respective original logs, and one female was found under a neighboring log at 1.7 m distance from her original log (Movement 4). These two females resided in logs at 215.7 and 214.0 m distances, respectively, from fishless pools. All but the four movements between logs were a single capture or a resident individual captured repeatedly from the same log [i.e., no movement was found in most of the recapture events in 2004–2005 (96.8 %, 121/125)].

Mean number of individuals sharing a log refuge in 68 observations on aggregation (=average aggregation size: Table 4) was  $2.85 \pm 0.15$  ( $\pm$  SE, range 2–9):  $2.27 \pm 0.12$  in 2004 ( $N_{\text{observations}} = 15$ , range 2–3) and  $3.02 \pm 0.18$  in 2005 ( $N_{\text{observations}} = 53$ , range 2–9). Mean maximum number of individuals sharing a log refuge on the same day (=sharing group size) was  $3.25 \pm 0.48$  in 2004 ( $N_{\text{days}} = 4$ , range 2–4) and  $4.80 \pm 0.66$  in 2005 ( $N_{\text{days}} = 10$ , range 3–9). Individuals exhibited a nonrandom residency in 40 logs for 2004 ( $N_{\text{individuals}} = 61$ ;  $\chi^2 = 163.918$ ,  $df = 39$ ,  $P < 0.0001$ ), 2005 ( $N_{\text{individuals}} = 239$ ;  $\chi^2 = 396.958$ ,  $df = 39$ ,  $P < 0.0001$ ), and 2004–2005 ( $N_{\text{individuals}} = 300$ ;  $\chi^2 = 380.465$ ,  $df = 39$ ,  $P < 0.0001$ ).

#### Aquatic larvae

In 2004–2005, because of early metamorphosis in summer, very limited numbers of aquatic larvae shortly before metamorphosis (i.e., characterized by degenerating gills and tail fins) were captured from sites 2 ( $N = 2$ ), 4 ( $N = 2$ ), and 5 ( $N = 6$ ) where aquatic macroinvertebrate predators such as backswimmers (Notonectidae spp.) and diving beetles (e.g., *Dytiscus dauricus*, *Dytiscus marginalis*, *Graphoderus zonatus*, *Rhantus* sp.) were present simultaneously, but fish did not exist. Fish predators, including the burbot (*Lota lota*) and the Eurasian minnow (*Phoxinus phoxinus*), were captured from sites 1, 3, and 6 where no salamander larvae were trapped. A large off-channel crescent lake was connected to the site 3 whenever rainy and was also regarded as fish-dwelling water. When comparing data between July 2004 and August 2005, larval

trapping rates in 2005 (measured as  $N/\text{day}$ ) were reduced to 0 % (site 2: from 0.50 to 0.00), 40 % (site 4: from 0.25 to 0.10), and 8 % (site 5: from 1.25 to 0.10) of the trapping rates in 2004.

In the follow-up survey on May 13, 2006, frozen road conditions allowed access to Darhadyn Wetland. The study area was partially covered with snow, and the Shishkhd River was mostly frozen. This freezing condition permitted us to walk across the river. In sites 1–6, the surface of the pond water was frozen in the morning but melted afternoon to some extent. There were no egg sacs deposited in these sites.

## Discussion

### Potential consequences of aggregation

Although it is unknown whether summer aggregation was a year-round phenomenon, our results show that individuals aggregated under downed logs for several days at a time during the summer months. Aggregation occurs when a restricted sheltering resource is forced on individuals (Chapple 2003; Heino and Soinen 2006; Hill et al. 2006). Our study of aggregation suggests that *S. keyserlingii* may tolerate conspecifics, may not exhibit territorial aggression, may be attracted to conspecifics, and may have significant opportunity for social interaction. Our data support such conclusions because: (1) salamanders were recaptured under the same logs, exhibiting site tenacity, in 96.8 % (121/125) of recapture events, (2) salamanders composed of several male–female pairs or aggregators remained under the same logs in a sharing group (maximum aggregators = 9), and (3) “site fidelity” (defined as a tendency to return to a previously occupied location: e.g., Marvin 2001) was observed in two females captured between years. These females likely migrated more than 200 m to the fishless breeding pools and then returned to/near their respective logs between years. It is possible, however, that these females did not breed in 2005 and thus never left their log refuge, or that their refuge choices were random.

If aggregation is the case in *S. keyserlingii*, what are the potential consequences of aggregation? It may be true that restricted habitat availability causes aggregation (e.g.,

**Table 3** Several examples of aggregation (columns) and site tenacity (rows) under downed logs by each sex or age class in 2005

| Site | <i>N</i> | Day |   |   |   |   |   |   |   |   |    |   |
|------|----------|-----|---|---|---|---|---|---|---|---|----|---|
|      |          | 1   | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |   |
| a    | 32       | U   | U | U | U | U | U | U | U | U | –  | – |
|      |          | J   | J | J | J | J | J | J | J | – | –  | J |
|      |          | –   | J | – | – | – | – | – | – | – | –  | – |
|      |          | –   | – | – | J | J | J | J | J | J | J  | J |
|      |          | –   | – | – | – | J | – | – | – | – | –  | – |
|      |          | N   | – | – | – | – | – | – | – | – | –  | – |
|      |          | N   | – | – | – | – | – | – | – | – | –  | – |
|      |          | –   | – | – | – | – | – | – | – | N | N  | – |
|      |          | –   | – | – | – | – | – | – | – | – | N  | – |
|      |          | –   | – | – | – | – | – | – | – | – | N  | – |
|      |          | –   | – | – | – | – | – | – | – | – | –  | N |
|      |          | –   | – | – | – | – | – | – | – | – | –  | – |
| b    | 27       | –   | – | – | – | M | M | M | – | – | –  |   |
|      |          | –   | – | – | – | – | – | M | – | – | –  |   |
|      |          | –   | – | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | – | – | – | – | – | M | M | M  |   |
|      |          | U   | – | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | – | – | – | – | J | J | J | J  | J |
|      |          | –   | – | – | – | – | – | – | – | J | J  | J |
|      |          | –   | – | – | – | – | – | – | – | – | –  | J |
|      |          | N   | – | – | – | – | – | – | – | – | N  | N |
|      |          | –   | N | – | – | – | – | – | – | – | –  | – |
|      |          | –   | – | N | – | – | – | – | – | – | –  | – |
|      |          | –   | – | – | – | – | – | – | – | N | N  | – |
| c    | 24       | U   | U | – | U | – | U | U | U | – | U  |   |
|      |          | –   | U | – | – | – | – | – | – | – | –  |   |
|      |          | J   | J | – | – | – | – | – | – | – | –  |   |
|      |          | J   | J | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | J | J | J | – | – | – | – | –  |   |
|      |          | –   | – | – | J | – | – | – | – | – | –  |   |
|      |          | N   | – | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | – | – | – | N | – | – | – | –  |   |
|      |          | –   | – | – | – | – | N | – | – | – | –  |   |
|      |          | –   | – | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | – | – | – | – | – | N | – | N  |   |
|      |          | –   | – | – | – | – | – | – | – | – | N  |   |
| d    | 20       | –   | M | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | – | M | – | – | – | – | – | –  |   |
|      |          | F   | F | – | – | – | – | – | – | – | –  |   |
|      |          | –   | F | – | – | – | – | – | – | – | –  |   |
|      |          | –   | F | – | – | – | – | – | – | – | –  |   |
|      |          | U   | U | – | – | – | – | – | – | – | –  |   |
|      |          | –   | J | – | – | – | – | – | – | – | –  |   |
|      |          | N   | N | – | – | – | – | – | – | – | –  |   |
|      |          | N   | N | – | – | – | – | – | – | – | –  |   |
|      |          | N   | N | – | – | – | – | – | – | – | –  |   |
|      |          | N   | – | – | – | – | – | – | – | – | –  |   |
|      |          | –   | – | – | – | N | N | N | – | – | N  |   |



**Table 3** continued

| Site | N  | Day |   |   |   |   |   |   |   |   |    |
|------|----|-----|---|---|---|---|---|---|---|---|----|
|      |    | 1   | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| e    | 18 | M   | M | M | – | M | M | – | M | M | –  |
|      |    | F   | – | F | – | F | – | – | – | – | –  |
|      |    | F   | – | – | – | – | – | – | – | – | –  |
|      |    | –   | – | – | F | – | – | – | – | – | –  |
|      |    | U   | – | – | – | – | – | – | – | – | –  |
|      |    | N   | N | – | – | – | – | – | – | – | –  |
|      |    | –   | N | N | – | – | – | – | – | – | –  |
|      |    | –   | N | – | – | – | – | – | – | – | –  |

Total numbers of individuals captured per log over the course of the study (N) were expressed in descending order. See Fig. 1 for sites a–e. M: adult males, F: adult females, U: unsexed individuals, J: juveniles (over one year old), N: metamorphs or newly metamorphosed juveniles (less than one year old)

**Table 4** Various types of habitation under 40 downed logs

| Type of habitation                 | Year |      |           |
|------------------------------------|------|------|-----------|
|                                    | 2004 | 2005 | 2004–2005 |
| Single habitation (no aggregation) | 26   | 76   | 102       |
| Aggregation                        | 15   | 53   | 68        |
| M–F pair                           | 0    | 1    | 1         |
| M–F pair with multiple U/J/N       | 0    | 1    | 1         |
| 1 M–multiple F with multiple U/J/N | 0    | 3    | 3         |
| 1 M with multiple U/J/N            | 1    | 11   | 12        |
| 1 F with multiple U/J/N            | 5    | 3    | 8         |
| Multiple M with multiple U/J/N     | 0    | 1    | 1         |
| Multiple F with multiple U/J/N     | 2    | 0    | 2         |
| Multiple U/J/N                     | 7    | 33   | 40        |

Each number indicates observed times in 2004 (4-day survey) and 2005 (10-day survey). Of the 300 capture events, 198 were aggregating (68 observations on aggregation were categorized in eight classes). See Table 3 for M, F, U, J, and N

butterfly *Pararge aegeria*: Hill et al. 2006), and such aggregation can play a role in the initial stages of the evolution of complex sociality (Chapple 2003). Selective factors that influence social decision points, which an individual makes throughout its life, include predation risk, dispersal/group joining, reproduction, and helping/cooperation (Helms Cahan et al. 2002; Komdeur 2006). Other selective factors include continuous refuge use, sharing, and aggregation (larger group size is more social in many animals, except for pair-living animals such as birds: Bulova 1994; Chapple 2003). Detecting aggregation is a first step in determining whether a species exhibits complex sociality. If aggregation is some form of complex sociality, what are the costs and benefits? As potential costs, aggregation may increase risk of disease transmission (e.g., Wilson et al. 2003). Also, there might be no benefit to aggregating, i.e., the salamanders may aggregate simply because downed logs have such limited availability.

One scenario that might be worth investigating for potential benefits is water conservation (Peterman et al. 2013) because our salamanders were in physical contact with each other. When amphibians aggregate during daytime in summer, they will decrease overall skin surface area exposure and thus limit water loss. This would provide some evidence for complex sociality.

“Cohabitation” (defined as two or more individuals simultaneously occupying the same refuge: e.g., Harless et al. 2009; but this term seems to contain sexual interaction), rather than aggregation, of conspecifics using refuges and their interactions are documented such that many members of the genus *Plethodon* have more complex social systems than those known in other amphibians (Anthony et al. 1997; Toll et al. 2000; Gillette 2003). In caudate amphibians, members of this genus are completely terrestrial and show direct development, and some maintain territories for access to food resources and mates (Petranka 1998). Territorial individuals move above ground to forage at night and hide in burrows or under logs during daytime. Cohabitation is also documented during the terrestrial-nonbreeding phase of migratory salamanders with internal fertilization, e.g., the long-toed salamander *Ambystoma macrodactylum* that spends more time in cohabitation in a burrow than residing alone when provided with a partner (Verrell and Davis 2003) and the great crested newt *Triturus cristatus* that resides in shelters with conspecifics (Malmgren et al. 2007). Although it is unknown whether our data on aggregation consisting of some male and female pairs or aggregators showed cohabitation, such cohabitation might occur just because of chance, or because both sexes select similar habitats (Ficetola et al. 2013).

#### Study limitations

The major limitations of our study are: (1) it was confined to a very short period (up to 10 days) during the summer

and (2) we did not sample in habitats beyond our 40 logs and thus could not really know the fate of marked individuals that were never captured again. Likewise, some other limitations are considered. Grassland located between logs could be a movement barrier for salamanders (Rittenhouse and Semlitsch 2006); thus, in a day when individuals were not recaptured beneath logs, they could be into decaying log spaces and might have moved to ca. 20 nonmonitored logs or in unfound, very small burrows from invertebrates. In contrast to the aforementioned within-year site tenacity, there were only three recaptures between years. Although the life expectancy is not well known for *S. keyserlingii* (Hasumi and Kanda 2007; Hasumi et al. 2009), individual mortality between years may be similar to other salamanders and should be relatively low. Thus, we suggest several other reasons for the low recapture rates. One explanation is that the number of marked individuals was very small in 2004 ( $N = 40$ ), which represented only a small portion of the larger population. Other explanations are that juveniles and metamorphs tended to disperse widely as in other migratory amphibians (Semlitsch 2008), and individual survival may be low due to severe environmental conditions at Darhadyn (see “Conservation measures”).

Daily surveys relative to weekly surveys significantly reduce recapture rates in some salamander species in North America (Monti et al. 2000; Marsh and Goicochea 2003; Bailey et al. 2004; D. J. Hocking, pers. comm.). Such a researcher-mediated effect on refuge use was not recognized at Darhadyn because despite daily surveys, salamanders showed repeated or continual use of the same logs over multi-day sampling periods across 2 years. This tenacity is reinforced with individuals’ foraging above ground at night remote from their original refuges (Hasumi and Kanda 2007). Although site tenacity to a specific refuge (e.g., rock crevice, burrow, tree hollow) is documented in several *Egernia* species of squamate reptiles (Chapple 2003) and a terrestrial salamander *Plethodon cinereus* (Gillette 2003), our finding of site tenacity to only log refuges was surprising because there is little literature to document such behavior in vertebrate taxa (Tallmon and Mills 1994). Clarifying potential costs and benefits of site tenacity to a specific refuge would contribute to our understanding of aggregation. Because there is no study that examines “kin recognition” (Chapple 2003) and “dear enemy recognition” (Jaeger 1981) in *S. keyserlingii*, further studies are needed to determine whether such recognitions occur within a sharing group of aggregation.

#### Conservation measures

*Salamandrella keyserlingii* is the widest ranging amphibian species (Borkin 1999) but is endangered in Mongolia

(Shiirevdamba 1997). At Darhadyn under a subarctic steppe–tundra climate, ambient air temperature could rise over 30 °C during daytime in summer (this study) and decreases to −49.9 °C during winter (Hasumi and Borkin 2012). Hence, this species had to possess adaptive and plastic traits for both hot and cold environments. These traits include: (1) downed log use by salamanders for refuge from hot summer temperatures (this study), (2) fall immigration, unrelated to mating, toward terrestrial hibernacula adjacent to aquatic-breeding locations although fall immigration is demonstrated in other portions of the species’ range, but not at Darhadyn (Hasumi and Kanda 2007), and (3) natural freezing tolerance against ambient air temperature down to −40 °C (Storey and Storey 1992). We suggest that using log refuges for summer aggregation is a main factor that has allowed *S. keyserlingii* to survive at Darhadyn: the permafrost detected at an underground depth of 1 m (N. Fuji, unpubl. data) has maintained summer temperature under downed logs around 10 °C that was cooler than in the air (around 17 °C).

Aquatic larvae of this species metamorphosed early at Darhadyn. Maybe this is adaptive because it allows them to get to appropriate refuges/hibernacula in a timely fashion, but it also exposes them to the extreme temperatures of summer. Therefore, it is even more important that downed log refuges would be available for shielding the tiny metamorphs from extreme summer temperatures. Actually, unusual abundance of metamorphs under log refuges from mid-July was caused by early metamorphosis and post-metamorphic dispersal. In Kushiro, Japan, metamorphs typically emerge in early September, and an “estimated premetamorphic period” (EPP) after the cessation of breeding activity is 3.5–4.5 months (Hasumi and Kanda 2007). Judging from the absence of egg sac deposition in mid-May, we estimated that the onset of the breeding season was, at the earliest, late May (EPP < 1.5 months, 1/3 of that at Kushiro). Although developmental time of aquatic larvae was not really known at Darhadyn where weather conditions could vary from year to year, apparently “early metamorphosis” relative to that at Kushiro (mid-July vs. early September) was observed, as documented at Shaamar, Mongolia (Hasumi et al. 2011). Aquatic larvae at Darhadyn may adopt a conditional tactic, whereby when winter temperatures in a region are relatively low, they metamorphose early, allowing them to reach optimal terrestrial hibernacula before extremely cold temperatures occur (minimum mean daily air temperature = −49.9 °C: Hasumi and Borkin 2012). Although larvae develop rapidly at Darhadyn, metamorphs grow slowly (Hasumi and Borkin 2012), leading to delayed sexual maturity in both sexes (5–6 years old), relative to early maturity of males (2–3 years old) and females (3–4 years old) at a warm population of Kushiro (mean

yearly air temperature = 7.98 °C: Hasumi 2010; Hasumi and Borkin 2012). An alternative hypothesis is that larvae metamorphose at a smaller size, meaning that even if they grow at the same pace as metamorphs at Kushiro, they just need longer to attain the same size. Among amphibians, there is commonly a trade-off between time of metamorphosis and size at metamorphosis (Rowe and Ludwig 1991). When larvae metamorphose early, they tend to be smaller and thus usually take longer to reach maturity. However, this alternative hypothesis is unlikely because larvae at Darhadyn metamorphose at the same size as that of Kushiro (around 30 mm SVL: Hasumi and Borkin 2012).

Downed logs were the only available refugia for salamanders at Darhadyn (i.e., 100 % use), and the logs' rarity leaves the salamanders more vulnerable to natural and human threats. Climate change, i.e., the progress of global warming, will cause the permafrost to melt, leading to higher temperatures beneath logs, making some logs unsuitable as refuges for *S. keyserlingii* (Hasumi et al. 2007). Besides a global warming threat, nomadic collection of downed logs that harvest for fuel wood and other uses such as housing (Aassve and Gereltuya 2002; Zhang et al. 2007) may also become a threat of the survival of this species although this factor did not influence the distribution of downed logs for terrestrial refuge of salamanders between 2004 and 2005. It is therefore essential for a conservation priority of log-associated amphibians (threatened by their communal behavior that seems relatively nonplastic because of their high site tenacity) to retain more decaying downed logs, offering refuges for the greater number of individuals.

## Conclusion

At Darhadyn, Mongolia, we observed aggregation and site tenacity under downed logs during the terrestrial-nonbreeding phase of *S. keyserlingii*. This aggregation and site tenacity resulted from restricted habitat availability, with downed logs being the only type of refuge available to this species at this location. Aggregation in the terrestrial phase could indicate complex social behavior for this species (see Chapple 2003). This finding had not yet been reported in the family Hynobiidae, a primitively extant family that practices external fertilization (Wells 2007). Our study thus extends knowledge of aggregation behavior in small vertebrate taxa generally and salamanders specifically. If restricted habitat availability can cause such aggregation in this family, we might have just observed the initial stages of the evolution of complex sociality. Social interaction is well documented in the aquatic-breeding phase for this family (Hasumi 2001a), but has not previously been

studied in the terrestrial phase. Therefore, an investigation into potential benefits or lack thereof of these associations would provide an interesting study of the evolution of complex sociality for small vertebrate and invertebrate taxa that use terrestrial refuges (e.g., Helms Cahan et al. 2002; Ebensperger and Blumstein 2006). Investigating the social behavior of *S. keyserlingii* and/or the experimental removal of refuges (e.g., Pike et al. 2011) is the next installment to this work.

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