

Spatial and temporal patterns of water loss in heterogeneous landscapes: using plaster models as amphibian analogues

W.E. Peterman, J.L. Locke, and R.D. Semlitsch

Abstract: Water balance is critical to survival, growth, and performance of many terrestrial organisms because it can influence foraging time, limit dispersal, and curtail courtship activities. Water loss can vary in time and space across the landscape, and can also be modulated by behavior. Amphibians are particularly sensitive to water loss because their skin provides little to no resistance to evaporative water loss. Our study sought to quantify rates of water loss across a heterogeneous landscape using plaster of Paris models as analogues for the Western Slimy Salamander (*Plethodon albagula* Grobman, 1944). Models were validated within a controlled laboratory setting prior to field deployment, and were shown to approximate rates and magnitudes of water loss observed in living salamanders. In the field, we tested both adult- and juvenile-sized models, and found that juvenile-sized models lost water at a greater rate under all contexts. The rates of water loss measured at night (1.5%/h–4.5%/h) was nearly half of those measured during the day (2%/h–10%/h). Rates of water loss were greatest on ridges with southwestern aspects during the day (5%/h–10%/h) and lowest in ravines with northeast aspects at night (1.50%/h–3.75%/h). The results of spatial and temporal patterns of water loss corroborate field observations of salamander activity patterns and distribution across the landscape, providing a physiological mechanism driving fine-scale habitat use and distribution. Although we tested plaster models as analogues for salamanders, this approach should be generalizable to other amphibian taxa, providing an efficient means of measuring rates of water loss in the field under biologically meaningful contexts.

Key words: desiccation, physiology, plaster of Paris, *Plethodon albagula*, Missouri, Ozark, Western Slimy Salamander.

Résumé : L'équilibre hydrique est essentiel à la survie, la croissance et la performance de nombreux organismes terrestres puisqu'il peut influencer sur le temps consacré à l'alimentation et limiter la dispersion et les activités de parade. La perte d'eau peut varier dans le temps et dans l'espace à l'échelle du paysage et peut également être modulée par le comportement. Les amphibiens sont particulièrement sensibles à la perte d'eau puisque leur peau ne résiste pas bien à la perte d'eau par évaporation. Notre étude visait à quantifier les taux de perte d'eau dans un paysage hétérogène à l'aide de modèles en plâtre de Paris comme analogues du pléthodone visqueux de l'Ouest (*Plethodon albagula* Grobman, 1944). La validité des modèles a été vérifiée en milieu contrôlé en laboratoire préalablement à leur déploiement sur le terrain, et il a été démontré que le taux et la magnitude des pertes d'eau qu'ils présentaient étaient approximativement les mêmes que ceux de salamandres vivantes. Sur le terrain, nous avons testé des modèles de taille adulte et juvénile et constaté que les taux de perte d'eau des modèles de taille juvénile étaient plus élevés dans tous les milieux. Les taux de perte d'eau mesurés la nuit (de 1,5 %/h à 4,5 %/h) étaient environ deux fois moindres que ceux mesurés le jour (de 2 %/h à 10 %/h). Les taux de perte d'eau les plus élevés ont été mesurés sur des crêtes d'exposition sud-ouest durant le jour (de 5 %/h à 10 %/h) et les plus faibles, dans des ravins d'orientation nord-est durant la nuit (de 1,50%/h à 3,75 %/h). Les distributions spatiales et temporelles des pertes d'eau observées corroborent les observations sur le terrain relatives aux motifs d'activité des pléthodons et leur répartition dans le paysage. La perte d'eau apparaît donc comme un mécanisme physiologique qui module l'utilisation de l'habitat et la répartition de l'espèce à petite échelle. Si les modèles de plâtre ont été utilisés comme analogues de salamandres, l'approche devrait pouvoir être généralisée à d'autres taxons d'amphibiens, fournissant ainsi un moyen efficace de mesure des taux de perte d'eau sur le terrain, dans des contextes pertinents sur le plan biologique. [Traduit par la Rédaction]

Mots-clés : dessiccation, physiologie, plâtre de Paris, *Plethodon albagula*, Missouri, Ozark, pléthodone visqueux de l'Ouest.

Introduction

Water balance is among the most critical of physiological factors affecting growth, survival, and performance of animals (Spotila 1972) and plants (Schulze et al. 1987). In topographically complex landscapes, distribution of water and humid atmosphere can be highly variable (Bennie et al. 2008). This variation often creates microclimates, which are areas where the local conditions differ from the broader surroundings. The distribution of these microclimates largely dictates the distribution and abundance of organisms across the landscape (Weiss et al. 1988; Scherrer and Körner 2011; Long and Prepas 2012). Furthermore, microclimates

can create refugia for organisms, allowing them to persist through habitat or climate alterations occurring at broader scales (Rittenhouse et al. 2008; Schmalholz and Hylander 2011). Gaining a clear understanding of how organisms lose water across the landscape can be exceptionally challenging. Collection and experimentation with living specimens may be logistically and ethically prohibitive, but these challenges do not reduce the importance of the knowledge that can be gained from such data.

Models have been used in place of living amphibians to derive empirical estimates for both operative temperature (Zimmerman and Tracy 1989; Bartelt and Peterson 2005; Tracy et al. 2007) and

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rates of water loss (Bartelt and Peterson 2005; Tracy et al. 2007), and have been constructed from a variety of materials including copper (Bartelt and Peterson 2005), aluminum (Schulze et al. 1987), agar (Spotila and Berman 1976), sponges (Hasegawa et al. 2005), and plaster (O'Connor 1989; Tracy et al. 2007). Especially for amphibians, evaporative water loss and water balance have long been identified as key factors dictating activity and habitat use (reviewed by Wells 2007). Amphibians are particularly unique because their skin provides little to no resistance to water loss, effectively making them a free water surface (Spight 1968; Spotila and Berman 1976). These characteristics closely tie amphibians to the local environment, often dictating where they can persist (Rittenhouse et al. 2009; Long and Prepas 2012), when and how far they can disperse (Semlitsch 2008; Bartelt et al. 2010), and how long they can forage (Feder and Londos 1984). Furthermore, rates of water loss are key components to mechanistic and biophysical models used to predict habitat use, movement, and response to changing environmental and climate conditions (Kearney et al. 2008; Bartelt et al. 2010; Gifford and Kozak 2012).

Our study was designed to measure the spatial and temporal variation of water loss across a topographically complex landscape inhabited by a terrestrial salamander. Secondly, we sought to extend and validate the use of plaster models as surrogates for plethodontid salamanders. Understanding patterns of water loss can provide critical insight into a physiological mechanism underlying ecologically relevant patterns of behavior, abundance, and distribution in the field. Plethodontid salamanders are typically associated with cool, moist habitats and are predominantly nocturnal with surface activity peaking during or after rain events (Petranka 1998; W.E. Peterman, personal observation). The nonrandom distribution across the landscape and selective activity periods underscore the importance of water balance in these amphibians; we predicted that the spatial and temporal patterns of water loss would corroborate distribution and abundance across the landscape. Specifically, we predicted that rates of water loss would be greatest on ridges that receive the most daily solar exposure and lowest in ravines with the least daily solar exposure. We also predicted that rates of water loss would be lowest at night. Lastly, we predicted that plaster of Paris salamander models would act as a free water surface and lose water at rates similar to live salamanders with similar surface areas.

Materials and methods

Constructions of plaster models

We made plaster of Paris models to simulate both adult and juvenile salamanders, which have low and high surface areas, respectively. Adult models were made by cutting a 70 mm length of 12.7 mm diameter PVC pipe in half lengthwise. Each half of the PVC mold was lined with Mylar paper to prevent the plaster from adhering to the PVC. The halves were then put back together, secured with duct tape, and one end was sealed with duct tape. Juvenile models were made by tightly wrapping a 70 mm × 40 mm piece of Mylar paper around a wooden dowel with a diameter of 7.5 mm. The Mylar paper was then wrapped in duct tape and one end was sealed before the wooden dowel was removed from the paper. We mixed four parts plaster with three parts water and the plaster mixture was then poured into the molds. No dyes or pigments were added to the plaster because all trials were run at night or within closed-canopy forests, so absorption–reflection differences between salamanders and models should not factor into water loss. Models cured at room temperature for 48–72 h before being removed from the mold. All models were then sanded to standardize final length; adult models were 70 mm and juvenile models were 60 mm. All models were then cured in a drying oven for 24 h at 70 °C. Upon removal from the drying oven, models cooled to room temperature before being weighed on a

portable digital balance (Durascale, My Weigh) and were uniquely marked using a permanent marker. All mass measurements for this experiment were made to the nearest 0.01 g using this portable balance, which gave us the necessary resolution since water loss measures recorded during this study ranged from 0.1 to 5.6 g (mean = 0.91 g).

The surface area of our models corresponded to salamanders of approximately 52 mm snout–vent length (SVL) and 69 mm SVL, weighing 2.25 and 7.25 g, respectively. These size estimates were calculated with the equation

$$\text{SVL} = 15.058 \cdot \ln(\text{mass}) + 39.568233$$

which was determined from length and mass measures of 233 Western Slimy Salamanders (*Plethodon albagula* Grobman, 1944) from the Daniel Boone Conservation Area (38.779°N, 91.388°W) in Warren County, Missouri, USA, and explained 94% of the variation. These standard length measures are in agreement with literature estimates for juvenile and adult size classes for *P. albagula* (Trauth et al. 2004).

Model validation

To validate the use and biological relevance of our plaster models, we conducted a water loss study under controlled laboratory conditions. Fourteen *P. albagula* were collected from the Daniel Boone Conservation Area. Each salamander was housed in an individual container (16 cm × 16 cm × 4.5 cm) lined with moist paper towels. Salamanders were weighed on the portable digital balance and then placed in individual cylindrical retaining cages made from 3 mm hardware cloth (14 cm long × 3 cm diameter). Salamanders were then left for 120 min at 25 °C and 50% humidity. After 120 min, each salamander was weighed and then returned to its container. Salamanders were returned to the field within 72 h of collection. This experiment was conducted in compliance with the University of Missouri Animal Care and Use Committee (7403).

Plaster models were tested under the same temperature and humidity conditions as salamanders. Prior to experimentation, each model was soaked in water for 24 h. Excess water was blotted from each model before weighing and models were placed in identical hardware cloth cages. Following 120 min, final mass measurements were made and the rate of percent water lost was calculated as

$$\frac{(\text{wet mass starting} - \text{wet mass ending})}{(\text{wet mass starting} - \text{dry mass})/\text{time}}$$

To calculate the rates of percent water loss for salamanders, the water content of each salamander was estimated using the linear equation:

$$\% \text{Water} = (-0.0168 \cdot \text{live salamander wet mass (g)}) + 0.8747$$

which was determined in an unrelated study by drying 19 sacrificed specimens to a constant mass for 120 h at 100 °C (T.M. Luhring, unpublished data). The model predicted salamander water content to within 1.26% ± 0.94% of the measured water mass ($R^2 = 0.70$, $p < 0.001$). We then fit linear models to the plaster model and salamander data, regressing percent water loss per hour on surface area. Surface area for models was the standard surface equation for a cylinder, whereas surface area for salamanders followed the equation of Whitford and Hutchison (1967):

$$\text{RSA} = 9.62 \cdot W^{0.614}$$

where RSA is the respiratory surface area (cm²) and W is the mass (g).

To determine if rates of water loss in models varied over time, 10 juvenile models and 10 adult models were deployed in the laboratory at 25 °C and 50% humidity for 8 h and were measured every 20 min. Data were analyzed using a generalized linear mixed model with model as a random effect, model size and time as fixed effects, and percent water loss at each 20 min interval as the response.

Landscape effects on water loss

Field trials to test rates of water loss were conducted at the Three Creeks Conservation Area (38.830°N, 92.286°W) in Boone County, Missouri, USA. This area is characterized by topography that varies from 180 to 250 m above sea level, creating a variety of slope-aspect features across the landscape. Using a 10 m digital elevation layer (<http://seamless.usgs.gov>) in ArcGIS version 9.3 (ESRI (Environmental Systems Research Institute), Inc., Redlands, California, USA), we identified regions of the landscape that were of northeast (NE) or southwest (SW) orientation (20°–70° and 200°–250°, respectively) and 10%–25% slope. These aspect and slope combinations were chosen to maximize variation in solar exposure and ambient surface temperature. Furthermore, we used the landform classification tool (Jenness 2006) implemented in the Topography Tools toolbox (Dilts 2010) to identify ridges, slopes, and ravines on the landscape. Plots were then established along linear transects at NE and SW aspects, as well as at ridge, slope, and ravine positions. At each position, two adult and two juvenile plaster models in hardware cloth cages were deployed: one on top of the leaf litter and one under the leaf litter for each size, respectively. A single iButton temperature data logger was also deployed at each position adjacent to the four plaster models, recording the temperature at the air–soil interface every 30 min. The iButton data loggers were housed within 50 mL vials to protect them from moisture and covered by leaf litter. Lastly, tests were run during the day and at night. Models were deployed along six transects. Two transects were run concurrently during a trial; all data were collected during three days and three nights (22 September – 23 October).

Statistical analyses

Data on water loss of plaster models were analyzed using generalized linear mixed models using SPSS version 17 (IBM, Chicago, Illinois, USA). The dependent variable in our analysis was the percentage of water lost by each plaster model, which we square-root-transformed to achieve normality. Independent variables in the linear model included aspect as a categorical variable (NE or SW), landscape position as a categorical variable (ravine, slope, or ridge), aspect × landscape position interaction, and position as a categorical variable (under or on top of leaves). Lastly, temperature was used as a continuous covariate in the analysis and date and transect were modeled as random effects. Adult- and juvenile-sized plaster models were analyzed separately for both day and night trial periods. All descriptive statistics are reported as mean ± SD.

Results

Comparison of plaster models with salamanders

Both juvenile and adult models lost water in a linear fashion over the 8 h period of observation (Fig. 1), with juvenile models losing water at a rate of 5.16%/h ± 5.96%/h, whereas adult models lost water nearly three times slower at a rate of 1.80%/h ± 1.70%/h. Under the 25 °C and 50% humidity laboratory conditions, the rates of percent water loss are equivalent to 0.082 ± 0.025 and 0.14 ± 0.022 g of water lost per hour for juvenile and adult models, respectively. The variation in intermodel rate of water loss increased with time (Fig. 1). The comparison of slopes and intercepts for lines fit to rates of water loss for models and salamanders did not differ significantly (Fig. 2; slope: $p = 0.15$; intercept: $p = 0.39$), indicating that models and salamanders lose water at the same

Fig. 1. Rates of water loss for juvenile and adult salamander models at 25 °C and 50% humidity in the laboratory. Measurements were made every 20 min for 8 h. Error bars are ±SE.

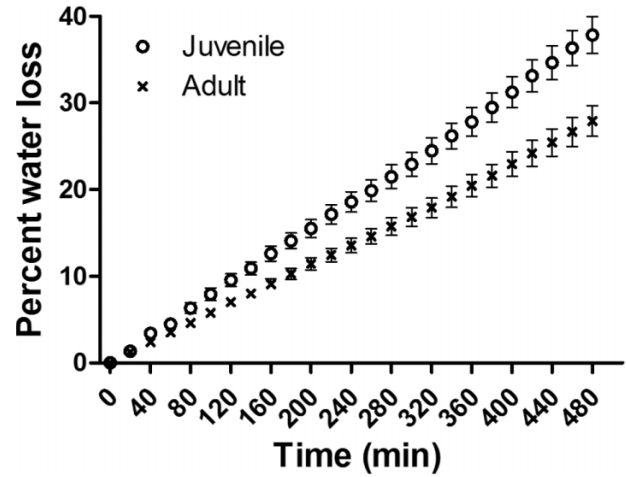
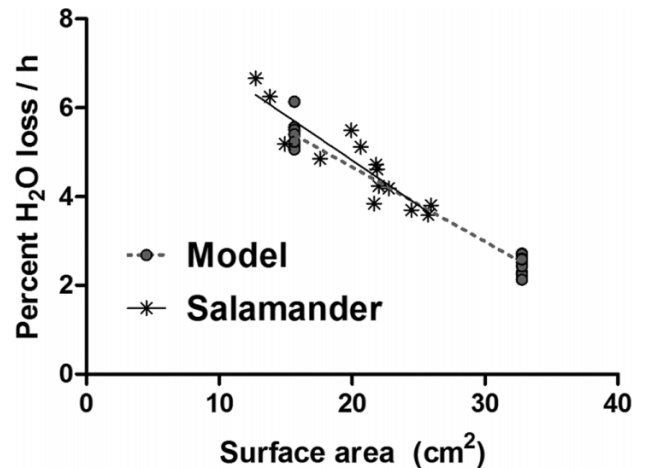


Fig. 2. Comparison of rates of water loss between Western Slimy Salamanders (*Plethodon albagula*) and plaster models in the laboratory. Trials were conducted for 120 min at 25 °C and 50% humidity.

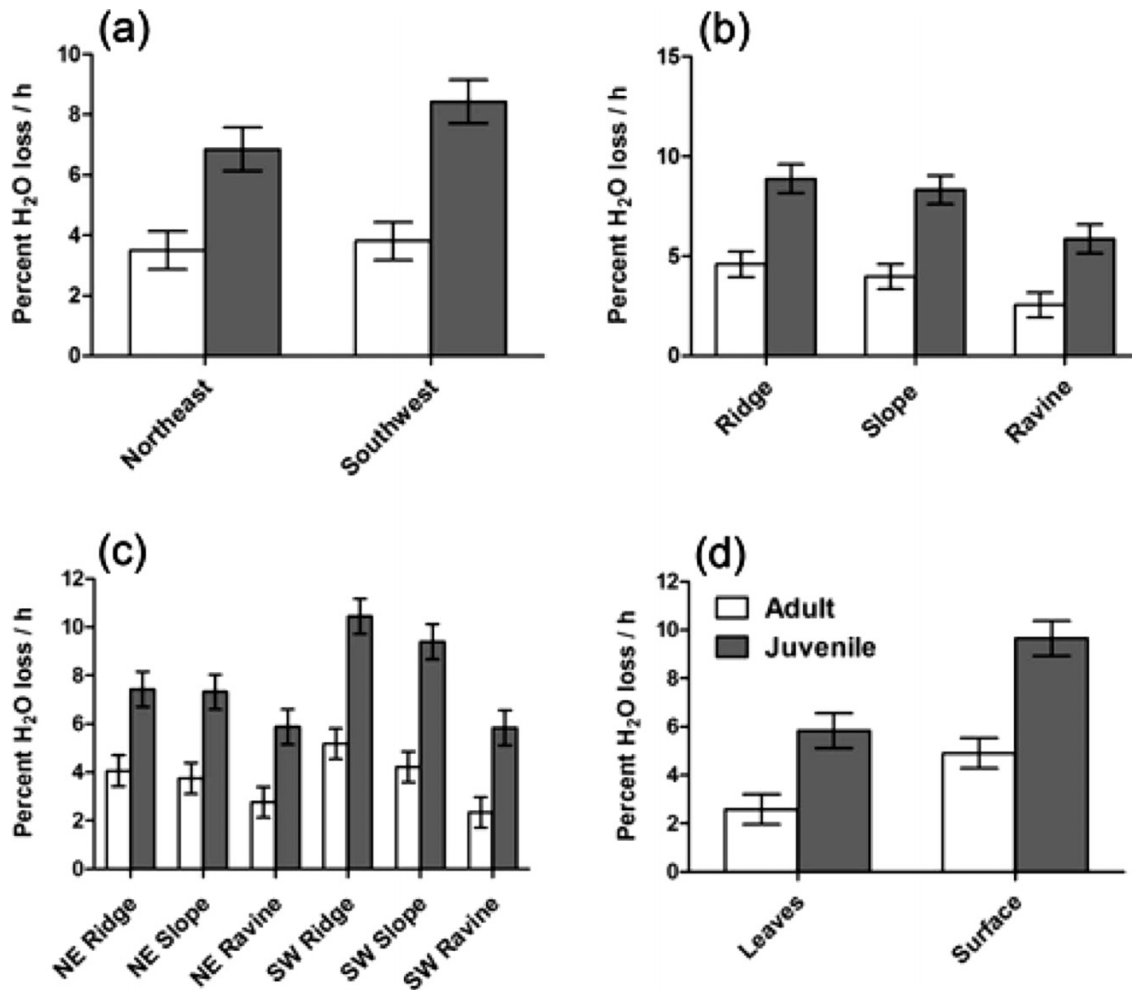


rate. Over the 2 h period, juvenile-size plaster models lost water at twice the rate of adult models (5.39%/h vs. 2.52%/h, respectively). The lack of significant difference between plaster models and salamanders, as well as the general linear trend in which water is lost from models, justified the use of plaster models as surrogates for salamanders in field experiments.

Water loss on the landscape

Juvenile models lost water at more than twice the rate of adult models at all locations assessed during both day (Figs. 3a–3d) and night (Figs. 4a–4d) trials. Overall, juvenile models were more sensitive to the assessed landscape variables with aspect and landscape position being highly significant, and the aspect × landscape position interaction approaching significance during the day (Table 1a). Adult water loss was significantly influenced only by landscape position (Table 1a) during the day, with models in ravines losing water at a significantly slower rate than slopes or ridges. In general, there was a stair-step pattern in the rates of water loss in relation to aspect, landscape position, and aspect × landscape position interaction, which was evident in both adult and juvenile models during the day (Figs. 3a–3c). SW aspects lost water at a greater rate than NE aspects, and ridge landscape positions lost water at a greater rate than ravine landscape positions. Rates of

Fig. 3. Rates of water loss of plaster models during daytime trials: (a) effect of aspect on water loss; (b) effect of landscape position on water loss; (c) interaction between aspect and landscape position; (d) effects of leaf cover on water loss. Error bars are \pm SE. Models were deployed within 1 h of sunrise, and water losses were measured 6–8 h later.



water loss in both adult and juvenile models were significantly affected by leaf cover during the day (Table 1a), but this treatment had no significant effect at night (Table 1b). In contrast to daytime water loss, no variables were significant at night for either adult or juvenile models. Landscape position exhibited a stronger effect for adult plaster models, but the effect was not significant (Table 1b). Temperature varied substantially across the landscape and from day to night. Daytime temperatures were, on average, about 4.5 °C higher than nighttime temperatures (17.65 ± 3.20 vs. 13.05 ± 1.62 °C). Daytime temperatures differed by aspect (NE = 17.00 ± 3.03 °C vs. SE = 18.29 ± 3.26 °C), as well as landscape position (ridge = 18.32 ± 3.11 °C vs. slope = 17.42 ± 2.90 °C vs. ravine = 17.20 ± 3.52 °C). Nighttime temperatures also differed by aspect (NE = 12.72 ± 1.49 °C vs. SE = 13.38 ± 1.69 °C), as well as landscape position (ridge = 13.28 ± 1.59 °C vs. slope = 13.11 ± 1.58 °C vs. ravine = 12.75 ± 1.68 °C). Temperature was a significant covariate only during the day for juvenile models and nearly significant for adult models, but temperature had no effect at night.

Discussion

Salamanders in the family Plethodontidae are lungless, respiring across the surface of their skin. For this gas exchange to be effective, these animals require relatively cool, moist habitats (Petranka 1998), and surface activity may be limited by their internal water balance, which has been called the “water time limit” (Feder and Londos 1984). Previous research has shown that salamanders

will voluntarily abandon surface activity and foraging at dehydration deficits (water loss) as low as 3.8% even though reductions in stamina, movement velocity, and total distance moved were not observed until >12% dehydration (Feder and Londos 1984), and mortality generally does not occur until dehydration deficits exceed 18% (18%–26%; Littleford et al. 1947). Our field observations of rates of water loss would suggest that daytime surface activity during our study would be limited to <1 h for juveniles and approximately 2 h for adults. At night, juvenile salamanders may be able to persist for 2–3 h depending upon location, whereas adults could persist for 4–8 h. These findings generally corroborate observations of occurrence among ridge, slope, and ravine habitats, as well as daily activity patterns in the field for *P. albagula* (Trauth et al. 2004; W.E. Peterman, unpublished data).

Although we conducted field trials during both day and night, salamanders are generally active on the surface at night (Petranka 1998), making our nighttime trials the most biologically relevant.

At night, we found no significant variation in water loss. One caveat of our study of plaster models in the field is that the study was conducted in the midst of a severe drought, so there was virtually no residual moisture in the soil or leaf litter and no salamanders were observed on the surface at this time (W.E. Peterman, personal observation). Whereas the gradient in rates of water loss during the day was most likely driven by daytime temperatures that varied due to solar exposure, at night the landscape became much more homogeneous with regard to surface temper-

Fig. 4. Water loss rates of plaster models during nighttime trials: (a) effect of aspect on water loss; (b) effect of landscape position on water loss; (c) interaction between aspect and landscape position; (d) effects of leaf cover on water loss. Error bars are \pm SE. Models were deployed within 0.5 h before sunset, and water losses were measured within 0.5 h after sunrise (\sim 12 h).

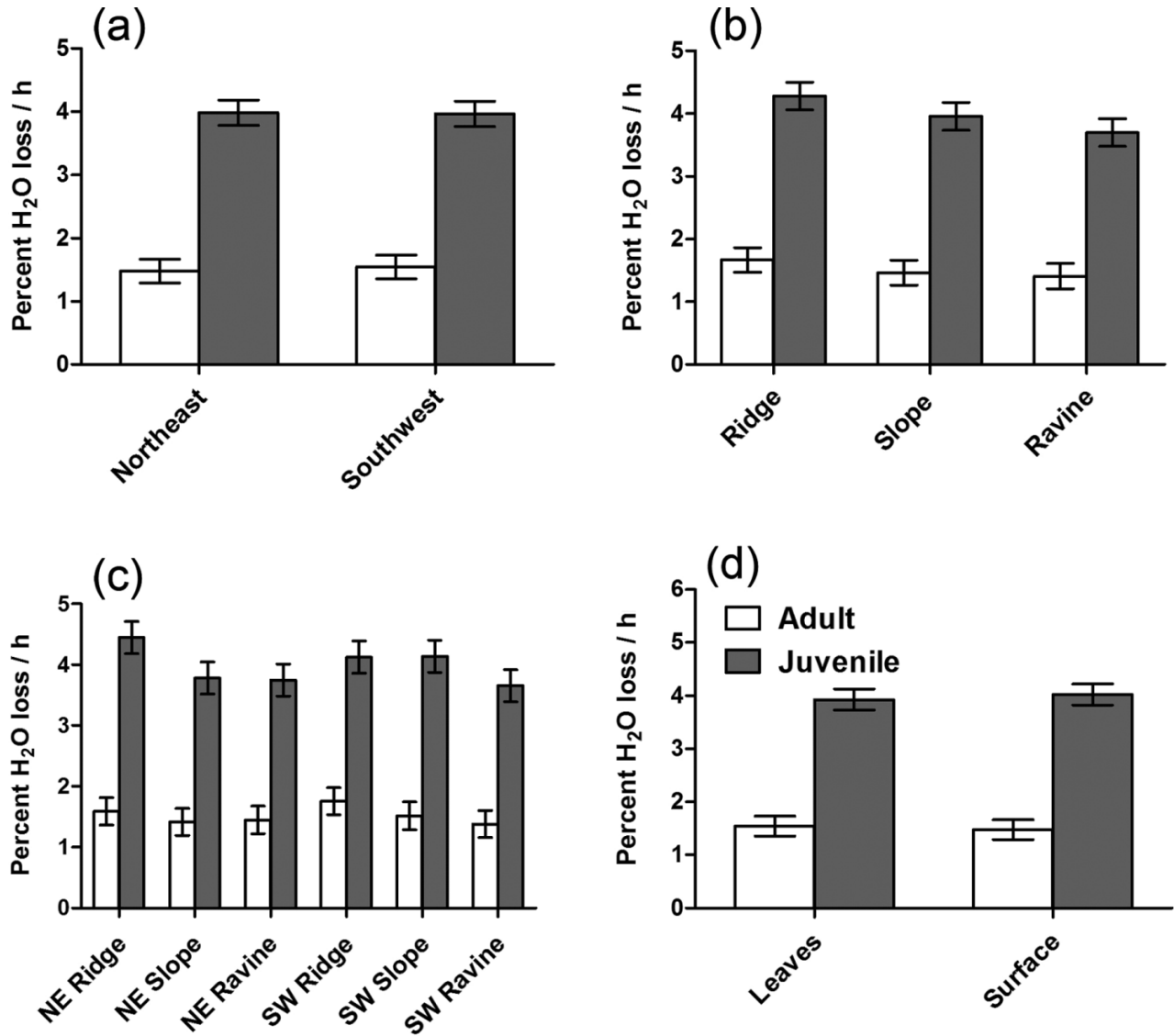


Table 1. Significance (*p* values) of parameters in mixed analysis for day (a) and night (b) trials of the Western Slimy Salamander (*Plethodon albagula*).

Parameter	Adult	Juvenile
(a) Day trial		
Intercept	0.203	0.136
Aspect	0.365	0.008
Landscape position	<0.001	<0.001
Aspect \times landscape position	0.168	0.089
Leaves	<0.001	<0.001
Temperature	0.067	0.027
(b) Night trial		
Intercept	0.009	<0.001
Aspect	0.491	0.949
Landscape position	0.057	0.114
Aspect \times landscape position	0.558	0.474
Leaves	0.480	0.662
Temperature	0.175	0.621

ature. We believe that this, in part, is a reason for the reduced variation in rates of water loss observed during the nighttime trials, but we predict that during seasons and conditions that are more favorable for salamander surface activity, similar significant gradients of water loss will be apparent during nighttime trials as those observed during our daytime trials. Even though salamanders are nocturnal, our daytime trials are relevant in that they quantify the potential consequences of being trapped on the surface during the day. Animals dispersing at night under optimal conditions will eventually expend their energy reserves and need to settle (Rittenhouse et al. 2009), and our trials demonstrate the consequences of these choices.

Our plaster models provided estimates of water loss comparable with those of salamanders under controlled laboratory conditions, giving us confidence that they could be deployed under field conditions to give biologically relevant estimates of water loss across the landscape. Because surface area is a critical component to the rate of water loss (Spight 1968), we tested both large and small models to represent adult and juvenile salamanders and found that they do lose water at significantly different rates. This is particularly relevant because juvenile

amphibians are generally considered to be the dispersing age class (Gill 1978; Gamble et al. 2007; Griffiths et al. 2010). It should be noted that our tests were conducted under only a single temperature and humidity, so we must make the assumption that rates of water loss will scale linearly as temperature and (or) humidity change. This is not an unreasonable assumption though, as Spotila (1972: Fig. 11) showed that water loss in salamanders was linear across a range of humidity.

Plaster models also have many practical advantages over live animals or models made from other media. First, models can be mass-produced at very little cost. Second, they are relatively durable and can be reused several times. Third, if color and reflectivity are important components to mimic for the assessment of operative temperature and water loss, plaster can be colored with cement dyes or paints (Tracy et al. 2007). Lastly, as has been previously discussed, water loss is a surface-area-dependent process. Thus, maintaining a constant surface area is essential for obtaining reliable estimates of water loss through time. Models made of agar can significantly shrink with time as water is lost, causing rates of water loss to vary (Tracy et al. 2007). We did observe an increase in the variation of water loss through time with our models as indicated by the increasing intermodel variance (Fig. 1), but the overall trend in water loss was linear with time. Tracy et al. (2007) noted a slight decrease in rates of water loss after 20% of available water had been lost. In our laboratory study, this corresponds with 4.5 h for juvenile models and 6 h for adult models (Fig. 1), but such an effect was not apparent in our study.

Understanding the physiological constraints imposed by the environment can provide mechanistic insight into the behavior, dispersal, and distribution of organisms, especially amphibians. Plaster models provide an efficient and effective means to quantify biologically relevant metrics. Although these models cannot dynamically account for individual behaviors such as water conservation postures and movement to reduce or avoid desiccation (Heatwole 1960; Spotila 1972), they can be shaped to mimic these postures (Tracy et al. 2007) to provide accurate and replicated measurements in situ. Future studies of water loss using these methods can interpolate results across the landscape to create spatial surfaces of water loss, which can provide the basis for experimentation, hypothesis testing, and simulation of movement and survival as they relate to population dynamics.

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