## RESEARCH

# The Survivorship and Water Loss of *Liometopum luctuosum* (Hymenoptera: Formicidae) and *Liometopum occidentale* (Hymenoptera: Formicidae) Exposed to Different Temperatures and Relative Humidity

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**ABSTRACT.** Two species of velvety tree ants, *Liometopum luctuosum* Wheeler, and *Liometopum occidentale* Emery (Hymenoptera: Formicidae), are commonly found in the western Unites States from Washington to southern California. *L. luctuosum* is restricted to coniferous forests in the mountains in the southern range, whereas *L. occidentale* is found in the lowlands. The survivorship of workers of both species exposed to several temperatures and relative humidity (RH) was determined. As temperature increased, survival of both species decreased. As the RH increased, survival of both species increased. However, *L. luctuosum* had higher overall survival in all treatment groups. The cuticular permeability (CP) and the rates of body water loss for each species were determined. Both species had similar CPs. Increased physiological tolerances of *L. luctuosum* may be an explanation for its broader distribution.

**Key Words**: velvety tree ant, cuticular permeability, saturation deficit

There are three North American species of *Liometopum*, known as velvety tree ants, found in the western Unites States: *Liometopum apiculatum* Mayr, *Liometopum luctuosum* Wheeler, and *Liometopum occidentale* Emery (Hymenoptera: Formicidae). *L. apiculatum* is restricted to the oak-pine-juniper woodlands of the southwest corner of the United States, in Colorado, Arizona, New Mexico, and Texas, and south into Mexico, from 1,512 to 2,450 m (Hoey-Chamberlain et al. 2013). The range of *L. luctuosum* extends from temperate habitats in British Columbia, Washington, and Idaho, south to Central Mexico, and east to Western Texas. This species inhabits pine, oak, Douglas fir, and juniper forests, sagebrush, and high-elevation riparian habitats (Hoey-Chamberlain et al. 2013). In New Mexico, it is typically found above 2,000 m, whereas *L. apiculatum* is most commonly found at lower elevations (Mackay and Mackay 2002). Within its range, *L. luctuosum* have been reported at elevations as low as 35 m in Washington and Oregon (L. D. Hansen, personal communication) up to elevations as high as 2,438 m in Mexico (de Conconi et al. 1983) and is often strongly associated with but not limited to pine trees (Del Toro et al. 2009). *L. occidentale* is found in lowlands and coastal regions from southern Washington to northern Mexico (Del Toro et al. 2009) at elevations as low as 7 m in Oregon up to 1,700 m in California (L. D. Hansen, personal communication). They are the most common and dominant ant in oak and pine forests of southwestern United States (Hoey-Chamberlain et al. 2013). In California, *L. occidentale* are also frequently collected in urban settings.

Little information is available on the thermal tolerance and survivorship of *Liometopum* species. Shapley (1920) reported that *L. occidentale* and *L. apiculatum* were active across a wide range of temperatures (8–38°C), humidity (5–100%), wind, and light. Temperature was the most important factor; the activity of these ants was very low, below 15°C (Shapley 1920). *L. occidentale* forages on hot days between 24 and 38°C in arid oak-digger pine woodlands (Tremper 1971). Both *L. luctuosum* and *L. occidentale* forage during the day in great numbers in the spring and early summer but around midsummer switch to nocturnal foraging.

The more wide spread distribution of *L. occidentale* at lower elevations, especially in southern California and Mexico, suggests this species might be more xeric adapted than *L. luctuosum*. The objective of this study was to determine if environmental factors such as temperature and relative humidity (RH) affect the distribution of each species. Live workers of both species were exposed to combinations of three different temperatures and RH found in their native environments, and survival of these workers was measured. In addition, the cuticular permeabilities (CPs) and water loss rates of both species were determined and compared with survival rates in experimental environments.

## Materials and Methods

**Ant Collections.** Foraging ants from three different colonies were collected for each species (Table 1). Colonies 1 and 2 of each species were ~4 km apart and at least 30 km from the third colony of each species. The collection sites in San Bernardino Co. had temperatures as low as –8°C in winter and as high as 37°C in the summer. The collection sites in Riverside Co. had temperatures as low as 0°C in winter and as high as 44°C in summer.

Ants were gently brushed off nest trees into collection boxes using a soft bristle brush. Boxes (~12 by 8 by 6 cm) were coated on the inside with Teflon T-30B (E.I. du Pont Nemours and Co., http://www.dupont.com/) to prevent ants from escaping. Ants were maintained in the laboratory (22.2–25.6°C) and sheltered in Petri dishes (14 cm in diameter) filled half full with plaster of Paris. They were fed 25% sucrose water three times a week and pieces of dead American cockroaches once a week; water was always available. The number of ants stored together in a single Petri dish varied from a couple hundred to over a thousand individuals.

**Exposure to Various Temperatures and RH.** The day before ants were exposed to our treatment conditions, ants were placed in groups of ~20 (17–22) in 236 ml polystyrene cups coated on the inside with Teflon to prevent them from escaping. Each group was provided water and 25% sucrose solution to ensure that all ants were well fed and hydrated. Three different levels of RH were maintained in glass desiccator jars with saturated salt solutions of magnesium chloride (32% RH), sodium dichromate (52% RH), and sodium chloride (75% RH) (http://www.fishersci.com, Winston and Bates 1960). The humidity chambers were then placed in three different environmental chambers

**Table 1. Collection sites for *L. luctuosum* and *L. occidentale***

| Species | Colony | Location |
|---|---|---|
| *L. luctuosum* | 1 | United States of America: CA, San Bernardino Co., Crestline, Lake Gregory Regional Park, 20 May 2012, 34° 14′25.62″ 117° 16′0.67″ W, Elevation 1,390 m |
| | 2 | United States of America: CA: San Bernardino Co., Crestline, Heart Rock near Camp Seeley, 3 August 2012, 34° 15′20.42″ 117° 19′50″ W, Elevation 1,280 m |
| | 3 | United States of America: CA: San Bernardino Co., Forest Falls, Mill Creek near Picnic Area, 3 August 2012, 34° 05′03.21″ 116° 53′51.68″ W, Elevation 1,645 m |
| *L. occidentale* | 1 | United States of America: CA: San Bernardino Co., Crestline, Lake Gregory Regional Park, 15 October 2011, 34° 14′28.94″ 117° 16′11.17″ W, Elevation 1,397 m |
| | 2 | United States of America: CA: San Bernardino Co., Crestline, Heart Rock near Camp Seeley, 3 August 2012, 34° 15′45.17″ 117° 16.56″ W, Elevation 1,280 m |
| | 3 | United States of America: CA: Riverside Co., Riverside, UC Riverside Campus, 19 August 2011, 33° 58′26.07″ 117° 19′47.48″ W, Elevation 321 m |

maintained at 15.6, 23.9, and 32.2°C. The saturation deficit (SD) for each chamber was calculated with the formula: SD = ([100 − RH]/100) * saturated vapor pressure (http://cronklab.wikidot.com/calculation-of-vapour-pressure-deficit). The number of dead ants was recorded every 12 h for 216 h.

**Water Loss Rates and CP.** CP and total body water (TBW) content of *L. luctuosum* and *L. occidentale* were determined gravimetrically. Ants stored in the laboratory were provided water and 25% sucrose solution the day before being selected for inclusion in this study to ensure they were well fed and hydrated. Ants were selected from boxes of ants stored in the laboratory and held overnight (12 h) with only water in a covered 236.6-ml cup coated on the inside with Teflon. This design maintained ants at 80% RH. The ants were killed by exposing them to KCN for 1 h. Ants were individually weighed to the nearest 1 µg (Sartorius M2P balance, http://www.satorius.com/) and placed in polystyrene weighing boats (2.54 by 3.81 cm). Twenty weighing boats of individual ants were placed in an 11-liter desiccator chamber containing about 0.7 kg anhydrous CaSO$_4$ (Drierite, W.A. Hammond Drierite Co. Ltd. Xenia, OH). The unstirred air in the chambers was maintained at 0–2% RH. The Drierite was conditioned by heating it for 4 h at 204°C to remove all water. The conditioned desiccators were maintained at 25.3 and 33°C for 24 h to ensure each chamber was stabilized before receiving specimens. These temperatures are within the natural temperature range in their native habitats. Ants were weighed individually at 2, 4, 6, 8, and 24 h and placed back into individual cups in the chamber.

The TBW for each species was determined by calculating the difference between the fresh and dry weight. After the 24-h exposure, dry weights were determined by moving the individual specimens to an environmental chamber maintained at 33°C and 0% RH. Specimens were weighed at day 7 and day 8, and the final weights were averaged. Weight loss was assumed to be entirely due to the loss of water.

CP of each ant was calculated as the difference in successive weights (wt$_1$–wt$_2$) divided by surface area (SA, cm$^2$), time (h), and SD (mmHg):

$$CP = (wt_1 - wt_2)/cm^2/h/mmHg,$$

and was expressed as µg of water lost cm$^2$/h/mmHg. Typically, the greatest water loss occurs in the first 2 h, and this was used to determine CP (Appel et al. 1983). Usually, SA is calculated from the fresh weight of the animal (wt in grams) by Meeh's formula where SA = $k$ (wt)$^{2/3}$, where $k$ represents a species or group-specific constant (Edney 1977). For cockroaches and other large insects, a $k$ value of 12 is often used (Appel et al. 1983). Haagsma et al. (1996) determined $k$ empirically for termites and nymphal cockroaches and derived the formula SA = 0.0886 + 26.85(wt) − 214.21 (wt)$^2$ where wt equals insect weight in grams. We also decided to use a third calculation of SA using the following formula: SA = 0.103(wt)$^{0.667}$ in which wt equals insect weight in milligrams and 0.103 = $k$, which was determined empirically by measuring the SA of the ant *Pogonomyrmex rugosus* (Lighton and

Feener 1989). The SDs of the chambers at 25.3 and 33°C were 23.8 and 37.7 mmHg, respectively.

**Statistical Analyses.** The effects of temperature, humidity, species, and colony on survivorship curves were compared using the Kaplan–Meier technique and log rank tests with a χ$^2$ approximation. Only ants that died during the observation period (216 h) were included in the analysis; those that survived for the entire period were "censored" from the data set (Cox and Oakes 1984). The direct and interactive relationships between mortality and humidity, temperature, and species were described with a Cox Proportional Hazard Regression (CPHR) model (SAS Institute 2007). Model selection was conducted using stepwise selection methods using SAS 9.2 to determine the best models in all cases.

Water loss data were best fit with nonlinear models. The effects of temperature, humidity, and species on percent water loss and CP were analyzed with analysis of variance and Tukey's HSD (honest significant difference) tests (Statistix 9 2011, http://www.statistix.com/). Some graphs were generated using SigmaPlot 12 (2010).

## Results

**Exposure to Various Temperatures and RH.** In general, survivorship declined more rapidly as temperature increased (log rank; χ$^2$ = 1,038.80, df = 2, $P < 0.01$, Fig. 1a); all three treatments differed from one another (Holm–Sidak: $P < 0.01$ for all comparisons). A similar trend was seen with declining humidity but was not as pronounced. Survivorship declined more rapidly at 32%, than at 52% or 75%, which did not differ significantly from one another (Fig. 1b; 32% vs. 52% and 75%: Holm–Sidak: $P < 0.01$; 52% vs. 75%: Holm–Sidak: $P = 0.09$). The survival curve of *L. luctuosum* was significantly greater than that of *L. occidentale* (Fig. 1c; log rank: χ$^2$ = 141.59, df = 1, $P < 0.01$).

The CPHR model, which includes both species and all the variables, was as follows: Time*Dead(0) = Temp + Hum + Specolony + Temp* Hum (likelihood ratio χ$^2$ = 1,715.52, df = 13, $P < 0.01$; Specolony = Species[Colony]). Using this model, the results were the same as in Kaplan–Meier log rank analysis, except all levels of RH were significantly different (Table 2). We also determined that most groups of ants were significantly different from each other, with the exceptions of ants from colony one and two of *L. luctuosum* and ants from colony two and three of *L. occidentale* (Table 2).

**Model With Both Species and SD.** The model was tested by removing the temperature and humidity component and utilizing the corresponding SD for analysis. The CPHR model, which includes both species and the variable SD, is as follows: Time*Dead(0) = SD + Specolony (likelihood ratio χ$^2$ = 1,715.52, df = 13, $P < 0.01$; Specolony = Species [Colony]). The survival rates of ants at the nine SDs were all significantly different from each other (Wald χ$^2$, $P < 0.01$), with the exception of survival rates in the SD 6.1 and. SD 5.6 treatments (Wald χ$^2$, $P = 0.34$). The survival rates of ants at the nine SDs were ordered, from highest survival to lowest survival, as
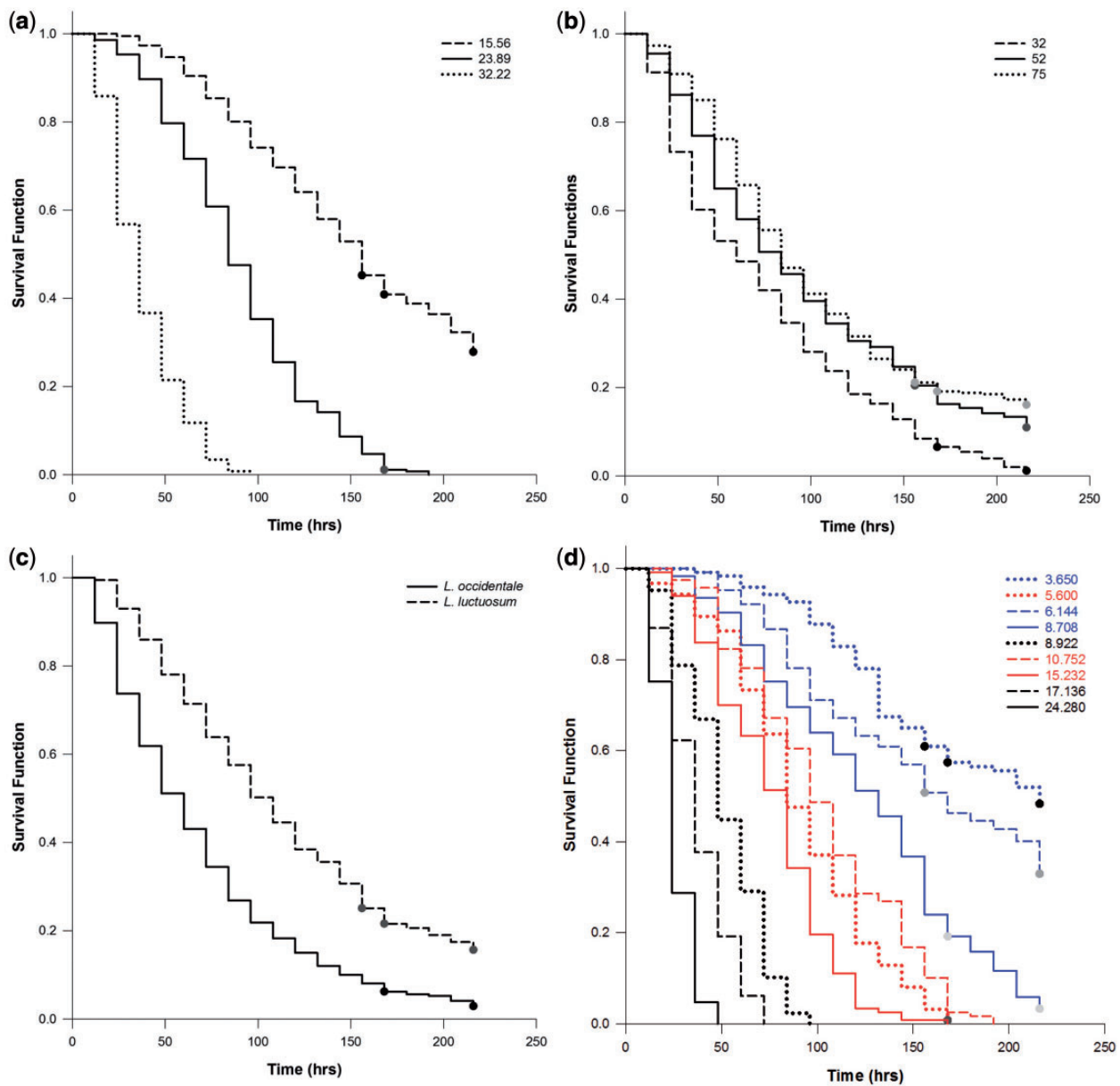
**Fig. 1.** Survivorships curves of ants across levels of (a) temperature, (b) humidity, (c) species, and (d) SDs.

**Table 2. The multiple comparisons of model factors for the model that includes temperature and RH: Time\*Dead(0) = Temp + Hum + Specolony + Temp\*Hum (likelihood ratio $\chi^2 = 1,715.5165$, df = 13, $P < 0.0001$; Specolony= Species [Colony]) with both species included in the model**

| Temperature | Humidity | *L. luctuosum* a | *L. occidentale* b |
|---|---|---|---|
| 15.56°C a | 32% a | C1 a | C1 a |
| 23.89°C b | 52% b | C2 a | C2 b |
| 32.22°C c | 75% c | C3 c | C3 b |

Temperature (T1–T3), humidity (H1–H3), and specolony (S1C1–S3C3). Within each column, treatment groups followed by different letters are significantly different ($P < 0.05$). Survivorship differed between both species (averaged across colonies), as well ($P < 0.01$).

follows: 3.650 (15.6°C, 75% RH), 6.144 (15.6°C, 52% RH), 8.708 (15.6°C, 32%RH), 10.752 (23.9°C, 52% RH), 5.600 (23.9°C, 75% RH), 15.232 (23.9°C, 32% RH), 8.922 (32.2°C, 75% RH), 17.136 (32.2°C, 52% RH), and 24.280 (32.2°C, 32% RH) (Fig. 1d).

**Water Loss Rates and CP.** On average, *L. luctuosum* individuals (weight: mean = 1.925 mg; range = 0.910–3.534 mg, $n = 39$) are significantly smaller than *L. occidentale* individuals (weight: mean = 3.962 mg; range = 1.437–5.238 mg, $n = 40$; *F* test, $P = 0.11845$). *Limetopum occidentale* had significantly higher initial body water content (68.9%) than did *L. luctuosum* (63.0%) ($F = 1.88$, df = 37, 39, $P = 0.03$).

Both species lost water at a faster rate at 33°C than at 25.3°C (*L. luctuosum*: Fig. 2; 25.3°C, $y = 0.028 + 0.025x$, $R^2 = 0.992$; 33°C, $y = 0.124 + 0.031x$, $R_2 = 0.886$; *L. occidentale*: Fig. 2; 25.3°C, $y = 0.099 + 0.025x$, $R^2 = 0.911$; 33°C, $y = 0.885 - 1.240x$, $R^2 = 0.971$). At both temperatures, the water loss rates for *L. luctuosum* were higher than those for *L. occidentale* (Fig. 2). Within 2 h at 33°C, *L. luctuosum* had lost 32.2% of its TBW compared with only 15.9% in *L. occidentale*.

Depending on the formula used to calculate SA, *L. luctuosum* and *L. occidentale* lost anywhere from 15.30 to 36.56 µg water/cm$^2$/h/mmHg. The CPs for both species were not significantly different at either temperature when using SA calculations by Haagsma et al.

(1996) (Table 3; $F = 1.47$, df 3, 74, $P = 0.2287$). Using SA calculations by Lighton and Feener (1989), we found that *L. occidentale* had the significantly lowest CP of both species at 25.3°C, *L. luctuosum* had the significantly highest CP of both species at 33°C, and that the CPs of these species at the other temperatures were intermediate (Table 3; $F = 5.50$, df 3, 74, $P < 0.01$). Using Meeh's SA calculation, we found that both species had significantly lower CPs at 25.3°C and significantly higher CPs at 33°C (Table 3; $F = 30.08$, df 3, 74, $P < 0.01$). However, we did not prefer this formula, as we felt that it greatly overestimated the SA of our species. Instead, we preferred the SA calculation by Haagsma et al. (1996), because this calculation is more conservative. *L. luctuosum* and *L. occidentale* had CPs that ranged from $17.01 \pm 6.46$ to $19.81 \pm 4.82 \mu g$ water/cm²/h/mmHg using our preferred formula.

## Discussion

Both species were negatively affected by increasing temperature and decreasing humidity; in both species, survivorship declined most rapidly at high temperatures and low humidity, and individuals lost more body water at higher temperatures and low humidity. These results support those of other researchers who have shown that survival time of ants decreases with decreasing humidity (Hood and Tschinkel 1990). These effects also varied between species, consistent with previous research showing that species differ in their desiccation resistance and survival (Hood and Tschinkel 1990). In addition, we demonstrated that populations also varied in their responses to temperature and humidity suggesting that thermal tolerances may vary with location.

Desiccation resistance depends on the rate of water loss and the amount of water that can be lost by individuals before there are any adverse effects (Schilman et al. 2007). TBW content of many ants varies between 60 and 70% (Hood and Tschinkel 1990). They can withstand losses of between 43 and 60% of their TBW and die when their TBW is between 40 and 54% (Hood and Tschinkel 1990). Arthropods

adapted to arid environments can withstand losses of 40–67% of their TBW without dying (Arlian and Wharton 1974, Toolson and Hadley 1977, Arlian 1979). Even though the larger species, *L. occidentale*, had significantly more TBW than the smaller species, *L. luctuosum* survival rates were higher with *L. luctuosum*. This contradicts patterns in other species, where smaller ant workers have significantly higher percentages of body water and significantly higher CPs than larger workers (Appel et al. 1991). However, like other species (Duncan and Lighton 1994, Schilman et al. 2007), smaller individuals of *L. luctuosum* and *L. occidentale* lost water at higher rates than larger individuals.

Insects have a number of physiological adaptations to xeric conditions such as minimizing the SA to volume ratio, controlling spiracular activity, depositing specialized cuticular hydrocarbons, reclaiming water and active water absorption, and producing metabolic water (Hadley 1972, Arlian and Veselica 1979). One of the major routes of water loss in ants is via the cuticle; only minor amounts of water are lost via respiration (Lighton and Feener 1989). The CPs of insects range from 0.3 to 190 $\mu g$ $H_2O$/cm²/h/mmHg with those between 20 and 60 considered to be mesic, and those under 20 $\mu g$ $H_2O$/cm²/h/mmHg considered to be xeric (Edney 1977, Schilman et al. 2007). Our results support findings from Tremper (1971), suggesting that *L. luctuosum* and *L. occidentale* are intermediate in their water loss, CPs, and responses to temperature compared with xeric species and mesic species (Tremper 1971). However, we also found that the water loss rates and desiccation resistance of *Liometopum* were more similar to desert ants. This supports results from Hood and Tschinkel (1990) that arboreal habitats are as stressful as desert habitats.

The montane species *L. luctuosum* has greater survival and a greater range in the northwest Unites States than *L. occidentale*. These results conform to Rapoport's rule that states distributional ranges of species increases with increasing latitude and altitude (Gaston et al. 1998). When the fact that montane species face extreme temperatures, precipitation, and other associated climatic events at higher elevations is also taken into consideration, our results support findings that montane habitats sustain species whose altitudinal ranges are larger (Stevens 1992).

As a side note, caution should be exercised when comparing CPs from different studies. Differences in CPs were greatly affected by the constants used to calculate SA. The equation generated by Haagsma et al. (1996) worked extremely well for insects <10 mg, and variances were very small for both *L. luctuosum* and *occidentale*. The equation generated by Lighton and Feener (1989) worked nicely for larger ants such as harvester ants, which are closer to 10–20 mg. Both equations provided very similar estimates of SA. However, the equation commonly used, SA = $k[\text{wt(g)}]^{0.667}$, where $k = 12$, overestimated the SA resulting in much higher CPs.

Both species of velvety tree ants are physiologically adapted to xeric habitats in the southwest and had similar CPs. However, *L. luctuosum* survived a greater range of temperature and RH conditions than did *L. occidentale*. The increased physiological tolerances of *L. luctuosum* may help explain its broader distribution. To survive montane conditions in the Southwest, greater physiological tolerances and ranges may be necessary. However, in more uniform urban habitats, this may detrimental to *L. luctuosum* resulting in the predominance of *L. occidentale*.
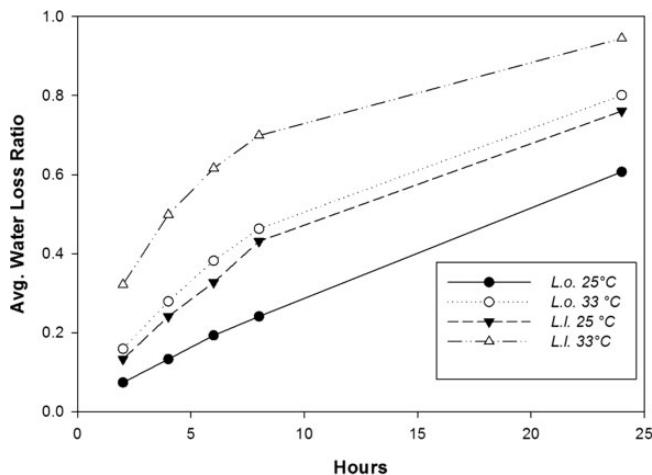


**Fig. 2.** The average water loss rates for *L. luctuosum* and *occidentale* at 25° and 33°C. The water loss rates for *L. luctuosum* are lower than *L. occidentale* at both temperatures.

**Table 3. The CP and percent TBW content of dead workers of *L. luctuosum* and *L. occidentale* exposed at 25 and 33°C**

| Species | Temp. (°C) | $n$ | Body water ratio (Avg. ± SD) | CPs[a] | CPs[b] | CPs[c] |
|---|---|---|---|---|---|---|
| *L. luctuosum* | 25.3 | 18 | 0.64 ± 0.08a | 17.76 ± 7.08a | 21.65 ± 9.01ab | 18.62 ± 7.75a |
| | 33 | 20 | 0.62 ± 0.04b | 19.06 ± 4.76a | 26.83 ± 8.65a | 36.56 ± 11.78b |
| *L. occidentale* | 25.3 | 20 | 0.70 ± 0.02a | 17.01 ± 6.46a | 17.79 ± 7.13b | 15.30 ± 6.13a |
| | 33 | 20 | 0.67 ± 0.03b | 19.81 ± 4.82a | 20.50 ± 4.68ab | 27.93 ± 6.38b |

[a] SA (cm²) = 0.09 + 26.85 (wt [g]) − 214.21 (wt [g])² (Haagsma et al. 1996).
[b] SA = 0.103 (wt [g])$^{0.667}$ (Lighton and Feener 1989).
[c] SA = $k$ (wt [g])$^{0.667}$ (Edney 1977; Appel et al. 1983, 1991).

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