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Water loss in desert ants: caste variation and the effect of cuticle abrasion

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Abstract. Water loss rates (WLRs) varied across castes (workers > alate males > alate females) for desert ants in the genera *Aphaenogaster, Messor* and *Pogonomyrmex*. Exposure to soil caused increased WLRs in workers and foundresses (mated, dealate females), apparently because of cuticular abrasion caused by nest excavation. Moreover, field-collected workers and foundresses from incipient nests (those exposed to soil) had similar WLRs, as did unabraded workers and alate females (those unexposed to soil). These data call into question previous adaptive scenarios for differences in WLRs across ant species and castes. For live alate females, WLRs increased over two stages. The first increase occurred immediately after mating, and the second occurred for foundresses collected 2 days later from incipient nests. By contrast, WLRs of HCN-killed females were unaffected by mating, but increased significantly for foundresses collected from 2-day-old nests.

Key words. Caste variation, colony founding, cuticle abrasion, myrmicine ants, nest excavation, water loss.

Introduction

Deserts present intense desiccation constraints for insects because of their small sizes and high surface to volume ratios (Hadley, 1994a). Free water is rarely available in deserts, so adaptations by which insects cope with these physiologically demanding environments typically involve mechanisms to conserve water. A waterproof layer of hydrophobic lipids often covers the insect cuticle, and thus provides one mechanism to conserve water. Limiting activity to cool portions of the day, and retreating to cooler, more humid subsurface areas when temperatures are high, is another such mechanism. Retreating to subsurface areas involves behaviours that range from seeking pre-existing shelters to excavating extensive underground galleries, such as nests dug by ants. One potential disadvantage for insects that dig regularly, however, is continued exposure to soil particles that can abrade the cuticle and cause increased water loss rates (WLRs) (Holdgate & Seal, 1956; Nel, 1965).

Physiological studies on water balance often focus on comparing WLRs between insects from different habitats. As might be expected, WLRs within related groups of insects are often positively associated with increasingly mesic conditions (Edney, 1977; Hadley, 1994a). Although interspecific comparisons of WLR are common, similar intraspecific comparisons between sexes or castes are rare (Toolson, 1987; Lighton *et al*., 1993; Gibbs *et al*., 1997; Chippindale *et al*., 1998; Gibbs *et al*., 1998).

Ants are ideal for examining intraspecific variation in WLR because colonies consist of one genetic unit comprised of three castes that experience differing selective regimes. Additionally, workers and foundresses of soil-nesting species are regularly exposed to the potential effects of abrasion while excavating nests. The typical colony cycle of soil-nesting species begins with a newly mated female (foundress) that initiates a colony by excavating a nest. The foundress metabolizes body tissue to support herself and brood until workers eclose, and continues to produce only sterile workers until the colony matures. At this point, alate reproductives are also produced. Following the appropriate cue, reproductives fly from the nest to mate. Females then remove their wings and excavate a nest to restart the cycle. Consequently, foundresses should experience intense selection to minimize water loss over the extended period before workers eclose. Indeed, females survive longer than do workers and males under desiccating conditions (Talbot, 1934; Whitford *et al*., 1976; Elzen, 1986; Lighton *et al*., 1993), but it is unclear whether differences are caused by WLR, body size, or both. In the seed-

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harvester ant *Pogonomyrmex rugosus*, the three-fold higher WLR and much smaller size of workers compared to females suggest both factors could be involved (Lighton & Feener, 1989; Lighton *et al*., 1993).

This study quantifies water loss across castes of several common desert ants and one inquiline species in the subfamily Myrmicinae. The genera *Aphaenogaster*, *Messor* and *Pogonomyrmex* are examined because they provide a comparative overview of desert ants. Two data sets are presented: (1) total WLRs for workers, alate males and alate females, and (2) a comparison of WLRs between workers and foundresses that have and have not been exposed to the abrasive effects of soil.

Methods

Animal collection and care

WLR was determined gravimetrically for all castes in five desert ants, *A. albisetosa* Mayr, *M. pergandei* (Mayr), *P. colei* Snelling, *P. occidentalis* (Cresson), *P. rugosus* Emery, and alate females of *P. barbatus* (F. Smith) and *P. salinus* Olsen. *Pogonomyrmex colei* is a workerless inquiline species in nests of *P. rugosus* and thus deviates from the above colony cycle, as foundresses do not excavate a nest or provision brood (Johnson *et al*., 1996). Individuals were collected from mature colonies in Arizona, Nevada and New Mexico during the mating flight season. This was late January to early March for *M. pergandei* and July to September for all others. Individuals remained in closed containers with *ad libitum* moisture prior to trials, such that WLRs are those for hydrated individuals. Except for laboratory-eclosed workers (see below), trials were conducted <72 h after capture and thus reflect natural WLRs because individuals did not have time to acclimatize to laboratory conditions (Lighton & Feener, 1989).

Cuticle abrasion

The potential effect of cuticular abrasion was examined by comparing WLRs of workers and foundresses that had and had not been exposed to soil. This involved comparing foragers to workers obtained from field-collected larvae that were eclosed and maintained in soil-free containers. WLRs of laboratory-eclosed workers were measured 1–2 weeks after individuals matured, as indicated by acquiring adult coloration. For females, dealate foundresses captured as they exited a mating aggregation were compared to those collected from incipient nests two days later. WLR for live alate females of *P. barbatus* that were captured as they flew into the mating aggregation was also measured.

Water loss rates

WLRs of live ants were determined using 10 individuals per caste from each of four colonies (eight in *M. pergandei*). WLRs of live and HCN-killed ants were also compared for each caste. This involved collecting 30 individuals per caste from one colony and then haphazardly dividing them into live and HCN-killed treatments; this method controlled for colony variation and test conditions. HCN-killed individuals were cooled to immobility, asphyxiated with CO_2 and exposed to HCN; this procedure minimized loss of liquids prior to HCN exposure. The oral cavity was then sealed with paraffin.

WLRs in flowing air were determined by enclosing ants individually in $20\,\text{mm} \times 7\,\text{mm}$ chambers made of rigid plastic tubes sealed at both ends with push-fit caps of stainless steel screen. Each trial included the three castes from one colony ($n = 30$) or one caste from four colonies ($n = 40$). In all tests, the chambers were weighed, an ant was inserted and the chamber was reweighed. Four columns were assembled by connecting the chambers in tandem using short lengths of flexible plastic tubing; each column contained a maximum of 10 chambers plus one empty control chamber. The columns were then placed in a constant-temperature room at 30 ± 0.5°C. Air desiccated by Drierite was forced through columns at a rate of $100–150\,\text{ml}\,\text{min}^{-1}$, as controlled by a needle valve and rotameter. A Vaisala HMT 31 humidity gauge documented that air exiting columns was $<3\%$ relative humidity. Chambers were examined after 1, 2 and 4 h for ants that had died, as indicated by inability to right themselves. Dead individuals were weighed at that time. WLR for these individuals was calculated using the time interval in which the individual was last observed alive. After 8 h, all other chambers were weighed to 0.01 mg on a Mettler AE 163 balance. Final mass was then adjusted by the mean change in mass of the four control chambers. Mass loss over 8 h was considered equivalent to water loss (Edney, 1977; Duncan & Lighton, 1994). Chambers were handled with only latex gloves or forceps.

Total water loss rate ($\mu g\,H_2O\,h^{-1}\,cm^{-2}\,Torr^{-1}$) was calculated using the formula $WLR = L/(S * T * K)$; L is μg water lost over 8 h, S is body surface area (original wet mass$^{0.67} * 12$; Edney, 1977), T is hours of exposure, and K is a value that standardizes for water vapour pressure saturation deficit in Torr (31.8 at 30°C and 0% relative humidity). This value yields an area-specific WLR divided by saturation deficit. For live ants, this calculation includes respiratory water loss through the spiracles. In resting, discontinuously ventilating ants, respiratory water loss is a minor component ($<5\%$) of overall water loss (Lighton & Feener, 1989; Lighton *et al*., 1993). Data were transformed, as necessary, to meet analysis-of-variance assumptions.

Results

WLRs for live individuals were lowest in alate females, intermediate in males and highest in workers of all species except *P. rugosus*, where male and female WLRs were similar. These differences remained significant ($P < 0.05$) after adjusting *P*-values using the sequential Bonferroni technique (Fig. 1). WLRs of alate females ranged from about 6 to 9 μg h^{-1} cm^{-2} $Torr^{-1}$, whereas those of workers ranged from 15 to 34 μg h^{-1} cm^{-2} $Torr^{-1}$. WLR was correlated with dry mass

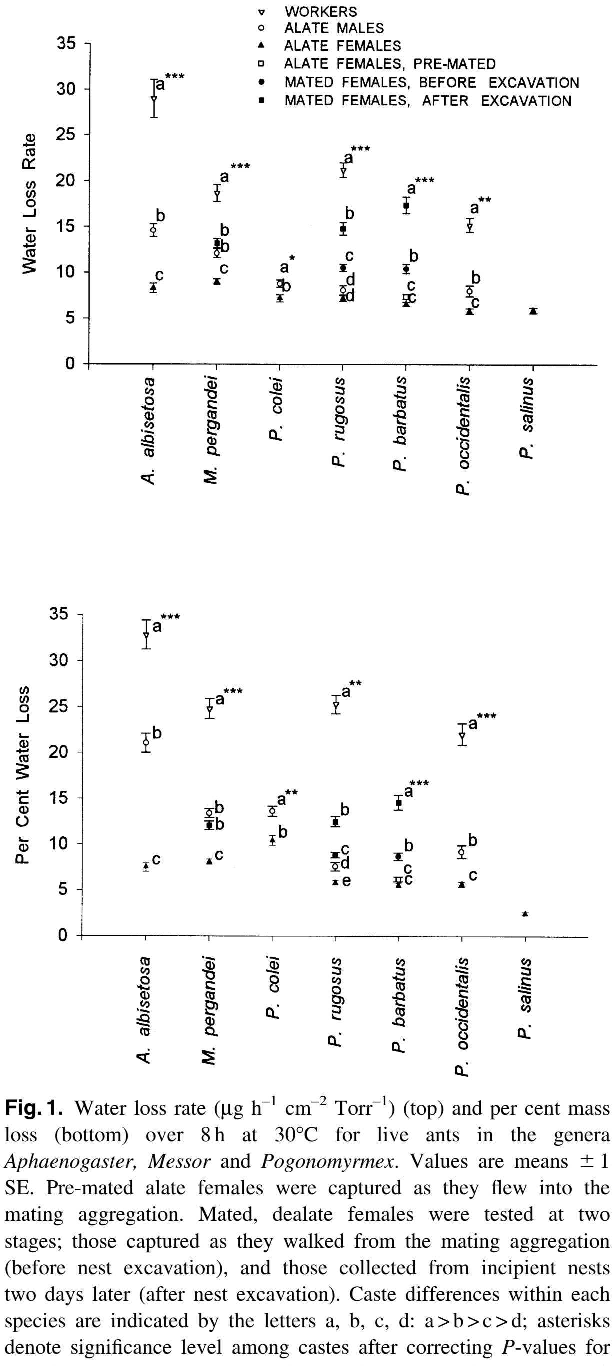

Fig. 1. Water loss rate ($\mu g\ h^{-1}\ cm^{-2}\ Torr^{-1}$) (top) and per cent mass loss (bottom) over 8 h at 30°C for live ants in the genera *Aphaenogaster, Messor* and *Pogonomyrmex*. Values are means ± 1 SE. Pre-mated alate females were captured as they flew into the mating aggregation. Mated, dealate females were tested at two stages; those captured as they walked from the mating aggregation (before nest excavation), and those collected from incipient nests two days later (after nest excavation). Caste differences within each species are indicated by the letters a, b, c, d: a > b > c > d; asterisks denote significance level among castes after correcting *P*-values for the six tests using the sequential Bonferroni technique. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$.

(mg) in *A. albisetosa* females ($y = -0.76x + 23.10$, $n = 39$, $R^2 = 0.19$, $P < 0.006$) and *M. pergandei* workers ($y = -4.52x + 28.22$, $n = 38$, $R^2 = 0.21$, $P < 0.004$). However, neither correlation was significant after adjusting *P*-values using the sequential Bonferroni technique. Additionally, WLR and dry mass were not correlated in a second trial that compared large (mean = 8.2 mg wet mass) and small (mean = 4.5 mg) *M. pergandei* workers (*t*-test, $n = 40$, t = 1.6, $P > 0.12$).

Table 1. Water loss rate ($\mu g\ h^{-1}\ cm^{-2}\ Torr^{-1}$) over 8 h at 30°C for live and HCN-killed female sexual ants in the genera *Aphaenogaster*, *Messor* and *Pogonomyrmex*. Values are means ± 1 SE; each test used 15 live and 15 HCN-killed individuals. Alates were excavated from their natal colony. Significant differences ($P < 0.05$) among female stages are denoted by the letters a, b, c: a > b > c. Asterisks denote significant differences between live and HCN-killed individuals after correcting *P*-values using the sequential Bonferroni technique; $^{*}P < 0.05$, $^{**}P < 0.001$

Species	Stage	Live	HCN-Killed
A. albisetosa	Alate	7.1 ± 0.6	11.0 ± 0.7**
M. pergandei	Alate	8.5 ± 0.5 b	11.0 ± 0.4 b**
	Foundress[1]	17.0 ± 1.8 a	16.6 ± 0.8 a
P. barbatus	Alate	5.9 ± 0.4 c	11.3 ± 0.3 b**
	Foundress[2]	10.3 ± 0.7 b	12.0 ± 0.5 b*
	Foundress[3]	15.2 ± 1.2 a	15.3 ± 0.9 a
P. rugosus	Alate	7.0 ± 0.2 c	12.1 ± 0.3 b**
	Foundress[2]	10.8 ± 0.4 b	12.4 ± 0.5 b*
	Foundress[3]	16.1 ± 0.8 a	14.9 ± 0.6 a
P. occidentalis	Alate	4.6 ± 0.3	8.6 ± 0.5**
P. salinus	Alate	6.1 ± 0.5	8.3 ± 0.2**

[1] Collected from incipient nests at an unknown interval after mating.
[2] Mated, dealate foundresses captured as they exited the mating aggregation.
[3] Collected from incipient nests 2 days after mating.

Expressing values as per cent loss of initial wet mass evidences ecological implications of these WLRs. For example, the small size of *P. colei* females (mean = 9.2 ± 0.1 mg wet mass) resulted in a two-fold higher per cent mass loss over 8 h compared to females of *P. barbatus* (mean = 48.5 ± 0.6 mg) and *P. rugosus* (mean = 53.5 ± 0.6 mg), even though WLRs were similar for all three species (one-way ANOVA, $P > 0.31$). Body size also effected intraspecific variation in desiccation-induced mortality for *M. pergandei* workers. Wet mass of workers that survived the 8 h trials was significantly higher (mean = 7.4 ± 0.2 mg) than for those that died (mean = 5.6 ± 0.3 mg, $n = 118$, *t*-test, t = 5.6, $P < 0.001$).

In all species, WLRs of live alates were significantly lower, by about 35–45%, than those of HCN-killed nestmates (*t*-test, $P < 0.001$, Tables 1 and 2). This difference occurred in workers of some species, but only when individuals were eclosed and maintained in the absence of soil (Table 3). By contrast, WLRs of field-collected workers were similar to, or higher than, those of HCN-killed nestmates (Table 2); higher WLRs in live workers were probably caused by activity during trials.

WLRs of live and HCN-killed females varied with stage in their reproductive cycle, and increased for both treatments after exposure to soil. In live *Pogonomyrmex* females, WLRs were lowest for alates from the nest and those flying into the mating aggregation, intermediate for mated, dealate females (foundresses) exiting the aggregation, and highest for foundresses from 2-day-old nests (Duncan's multiple-range test, $P < 0.0001$; Fig. 1, Table 1). For HCN-killed females, WLRs were lowest for alates and foundresses exiting the aggregation and significantly higher for foundresses from 2-day-old nests

Table 2. Water loss rate ($\mu g\,h^{-1}\,cm^{-2}\,Torr^{-1}$) over 8 h at 30°C for live and HCN-killed alate males and worker ants in the genera *Aphaenogaster*, *Messor* and *Pogonomyrmex*. Values are means ± 1 SE. See Table 1 for sample sizes and significance levels. ND = No data.

	Alate males		Workers	
Species	Live	HCN-Killed	Live	HCN-Killed
A. albisetosa	13.0 ± 0.6	16.2 ± 1.0**	16.2 ± 0.5	16.2 ± 0.5
M. pergandei	10.1 ± 0.7	17.1 ± 0.6**	19.5 ± 1.1	11.3 ± 0.8**
P. barbatus	8.5 ± 0.8	18.5 ± 0.6**	14.7 ± 1.0	12.4 ± 0.7
P. rugosus	9.2 ± 0.5	14.7 ± 0.8**	18.4 ± 1.2	17.8 ± 0.5
P. occidentalis	7.8 ± 0.7	13.7 ± 0.4**	17.5 ± 1.3	13.7 ± 0.9*
P. salinus	ND	ND	19.4 ± 1.8	19.1 ± 1.3

($P < 0.001$; Table 1). Moreover, WLRs of live foundresses exiting the aggregation increased relative to alates, but remained significantly lower than those of comparable HCN-killed foundresses ($P < 0.05$; Table 1). By contrast, WLRs were similar for live and HCN-killed foundresses from 2-day-old nests ($P > 0.22$). For *M. pergandei* females, WLRs were also lower for live and HCN-killed alates than for foundresses collected from incipient nests (*t*-test, $P < 0.001$; Fig. 1). Overall, WLRs of *Pogonomyrmex* and *Messor* females increased 2–2.5-fold in the days following mating.

Exposure to soil also increased WLRs of live and HCN-killed workers. For live workers, WLRs were significantly higher for field-collected individuals compared to those eclosed and maintained in the absence of soil (Tables 2 and 3) (*P. barbatus*: *t*-test with *P*-values adjusted using the sequential Bonferroni technique, t = 3.6, 26 d.f., $P < 0.002$; *P. occidentalis*: t = 11.3, 78 d.f., $P < 0.001$). This pattern also occurred in HCN-killed workers eclosed in the laboratory vs. those collected in the field (*P. barbatus*: t = 3.7, 28 d.f., $P < 0.002$; *P. occidentalis*: t = 4.8, 33 d.f., $P < 0.001$).

Discussion

Exposure to soil effected increased WLRs in live and HCN-killed worker and female ants. Such increases probably result from cuticular abrasion, which can damage the waterproofing wax layer of the cuticle and decrease hydrocarbon surface densities (Hadley, 1994a). Laboratory exposure to abrasive particles increases WLRs in worker ants (Nel, 1965) and other insects (Wigglesworth, 1945; Collins, 1969), but few data are available on occurrence and magnitude of the effects of abrasion under natural conditions. This study shows that abrasion can effect a 2–3-fold increase in WLR under natural conditions.

Cuticular abrasion confounds interpreting comparative studies that examine adaptive scenarios for differences in WLRs across ant species and castes. For example, Hood & Tschinkel (1990) found lower WLRs in arboreal than terrestrial ant species, with this difference presumably adaptive because arboreal species experience more desiccating conditions. An alternative explanation is that arboreal ants experience minimal cuticular abrasion because they rarely excavate nests, but rather use pre-existing galleries formed by termites and beetle larvae (S. P. Cover, personal communication). Effects of moving through tunnels would also be reduced for arboreal species because wood is much less abrasive than soil. Thus, the level of cuticle abrasion may have caused these habitat differences in WLR rather than differences in epicuticular lipids, as was hypothesized.

Table 3. Water loss rate ($\mu g\ h^{-1}\ cm^{-2}\ Torr^{-1}$) over 8 h at 30°C for live and HCN-killed worker ants collected as larvae and eclosed and maintained in the absence of soil. Values are means ± 1 SE (N); each row represents individuals from one colony. *$P < 0.001$.

Species	Live	HCN-Killed
Messor pergandei	7.1 ± 0.8 (9)	
Pogonomyrmex occidentalis	6.5 ± 0.6 (10)	11.0 ± 0.6 (9)*
	5.8 ± 0.5 (15)	5.9 ± 0.7 (11)
Pogonomyrmex barbatus	10.1 ± 0.9 (14)	9.1 ± 0.5 (15)

At the intraspecific level, caste variation in WLRs follows a consistent pattern in desert ants, being highest in workers, intermediate in males and lowest in alate females. Significantly lower WLRs (or per cent water loss) in alate females compared to workers have been used to argue for adaptive variation among castes that results from greater selection pressure on female sexuals (Talbot, 1934; Whitford *et al.*, 1976; Elzen, 1986; Lighton *et al.*, 1993). This study found that field-collected workers and foundresses from incipient nests had similar WLRs, as did unabraded workers and alate females. In the latter comparison, similarity between groups suggests that desert ants lack adaptive caste variation in WLR, and that the variation shown in other studies probably resulted from comparing unabraded alate females to cuticle-abraded workers (Elzen, 1986; Lighton & Feener, 1989; Lighton *et al.*, 1993). Moreover, intra- and interspecifc comparisons of WLR in ants, and probably other soil-dwelling invertebrates, are only valid when using unabraded individuals.

In ants, increased WLRs caused by abrasion are probably most important for foundresses, as this is the most vulnerable stage for a colony (Hölldobler & Wilson, 1990; Herbers, 1993; Johnson, 1998). Most desert ants have mating flights following summer rains and foundresses soon encounter desiccating conditions because soil moisture rapidly declines without additional rain (Nobel, 1988). Consequently, desiccation has the potential to be a significant source of foundress mortality in desert ants (Johnson, 1998; R. Johnson, unpublished data). The level of cuticular abrasion is important under desiccating conditions because WLR and survival time are inversely correlated (Gibbs *et al.*, 1997). For *P. occidentalis*, an increase in WLR from $5.8\,\mu g\,h^{-1}\,cm^{-2}\,Torr^{-1}$ in alates to $10.0\,\mu g\,h^{-1}\,cm^{-2}\,Torr^{-1}$ in recently mated foundresses caused mean survival time in dry air to decrease from 62.0 to 27.8 h (R. Johnson, unpublished data). Abrasion may also affect pleometrotic species (those with cooperating foundresses). For example, in the leaf-cutter ant *Acromyrmex versicolor*, one foundress specializes on nest digging activities (Rissing *et al.*, 1989), suggesting that this individual may incur a disproportionate increase in WLR caused by abrasion.

All castes displayed lower WLRs in live compared to HCN-killed individuals. However, this pattern depended upon cuticle integrity, as abrasion removed such control. This pattern was consistent across species for alate males and females. However, the pattern was sporadic for workers eclosed and maintained in the absence of soil, occurring in some species but not others, and in some colonies within a species but not others (Table 3). The cause of this variation is unknown.

Several potential mechanisms have been suggested to cause lower WLRs in live compared to HCN-killed individuals (Hadley, 1994a). In *Pogonomyrmex* females, mating results in physiological and behavioural changes, such as increased aggression, that are probably mediated by hormones. Increased WLRs for live females exiting, relative to those entering, the mating aggregation suggest that some mechanism related to vital state (possibly hormones) is involved in regulating water balance in ants. Cuticle damage caused by mating might cause this increase, but WLRs of HCN-killed females did not change over this interval, as would be predicted by this scenario. Moreover, physiological or behavioural changes associated with mating partially decrease control of WLR in live individuals, independent of the effects of cuticle abrasion.

This study focused on total water loss in these ants to assess water balance in an ecological context. Consequently, the WLRs reported here include cuticular and respiratory transpiration. Avenues of non-cuticular water loss include the mouth, anus and spiracles. That WLRs do not decrease when the mouth and anus are sealed suggests both orifices are minor avenues of water loss (Quinlan & Hadley, 1983; Lighton & Feener, 1989). This study also suggests that the mouth is a minor avenue of water loss in these ants, as WLRs of HCN-killed individuals (with mouths sealed with wax) were typically higher than those of live individuals.

Respiratory water loss through spiracles typically accounts for a low percentage of total water loss in quiescent insects (Hadley, 1994a,b). This pattern also occurs in ants, as respiratory transpiration accounts for $<5\%$ of the total water loss in workers of *P. rugosus* and *P. occidentalis* (Lighton & Feener, 1989; Quinlan & Lighton, 1999) and other ants (Lighton, 1992). By contrast, at 13%, the respiratory contribution to total water loss is much higher in alate females of *P. rugosus*. Lighton *et al*. (1993) suggested that the higher contribution of respiratory transpiration reflects the extremely low cuticular permeability of these females, thus increasing the percentage lost through transpiration. This caste difference in respiratory water loss is associated with level of abrasion: as level of abrasion, and hence cuticular permeability increases, the relative contribution of respiratory water loss probably decreases. Moreover, water loss via respiration comprises a low fraction of total water loss in these ants, suggesting that WLRs in this study approximate cuticular permeabilities (see Hadley & Quinlan, 1993; Hadley, 1994b).

In conclusion, age, task and caste have the potential to effect WLR in ants, suggesting that inter- and intraspecific comparisons of an adaptive nature are much more complicated than previously realized. This study shows that WLRs can increase quickly and are highest for individuals most susceptible to water deficits, i.e. foragers exposed to high vapour saturation deficits and claustral foundresses. Consequently, it may be more profitable to examine the water balance of ants in an ecological, rather than an adaptive context. For example, examining water and energy balance in foundresses will help the understanding of survival patterns of incipient colonies (see Johnson, 1998). Likewise, the water balance of adult nests should be examined to determine why species such as *M. pergandei* forage daily, whereas species such as *P. rugosus* typically cease foraging during extended xeric conditions (see Feener & Lighton, 1991; Duncan & Lighton, 1994; Lighton *et al*., 1994).

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