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Respiratory and cuticular water loss in insects with continuous gas exchange: Comparison across five ant species

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Abstract

Respiratory water loss (RWL) in insects showing continuous emission of CO_2 is poorly studied because few methodologies can measure it. Comparisons of RWL between insects showing continuous and discontinuous gas exchange cycles (DGC) are therefore difficult. We used two recently developed methodologies (the hyperoxic switch and correlation between water-loss and CO_2 emission rates) to compare cuticular permeabilities and rates of RWL in five species of ants, the Argentine ant (*Linepithema humile*) and four common native ant competitors. Our results showed that RWL in groups of ants with moderate levels of activity and continuous gas exchange were similar across the two measurement methods, and were similar to published values on insects showing the DGC. Furthermore, ants exposed to anoxia increased their total water loss rates by 50–150%. These results suggest that spiracular control under continuous gas exchange can be as effective as the DGC in reducing RWL. Finally, the mesic-adapted Argentine ant showed significantly higher rates of water loss and cuticular permeability compared to four ant species native to dry environments. Physiological limitations may therefore be responsible for restricting the distribution of this invasive species in seasonally dry environments.

Keywords: *Linepithema humile*; Gas exchange; Water loss; Cuticular permeability; Respiratory water loss; Biological invasion

1. Introduction

Water is essential for life; animals contain a high proportion of water. Since terrestrial animals live in a medium (air) that contains thousands of times less water than themselves, they should possess effective mechanisms to prevent desiccation by passive loss of water. Because of their large body surface area to mass ratios, terrestrial arthropods are especially susceptible to dehydration (Chown, 2002; Edney, 1977; Hadley, 1994). This is particularly true for water loss through the cuticle of terrestrial insects, but other sources may also contribute to desiccation (e.g., water loss through the spiracles when insects exchange gases during respiration).

The importance of respiratory water loss (RWL) in insects is controversial. It has been claimed in the literature that the cuticle is the primary route of water loss in terrestrial arthropods, and that RWL is such a small component of total water loss that it can be ignored (Edney, 1977; Hadley, 1994). For example in four ant species expressing discontinuous gas exchange cycles (DGC), the RWL rate varied between 2–8% of total water loss (Lighton, 1992; Quinlan and Lighton, 1999). Moreover, data from more than 20 species of insects from four different orders show that RWL is less (and usually much less) than 20% of total water loss (see Table 1 from Chown, 2002). As a consequence, many authors have concluded that modulation of such a small contribution is unlikely to represent a fitness benefit

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Table 1
Masses and catabolic flux rates

Ant species	Temp. (°C)	N	Individual mass (mg)	V CO$_2$ (μl h^{-1} ant^{-1})	MR (μW)	SMR (μW)	MR vs. SMR Paired t-test	Q_{10}
Forelius mccooki	20	6	0.274 ± 0.052	0.26 ± 0.04	1.52 ± 0.21	0.61 ± 0.10	$t_5 = 14.488$, $P < 0.0001$	
	30	6	0.278 ± 0.014	0.59 ± 0.10	3.45 ± 0.57	1.24 ± 0.06	$t_5 = 9.168$, $P = 0.0003$	2.02
	40	6	0.266 ± 0.020	1.05 ± 0.05	6.13 ± 0.68	2.39 ± 0.16	$t_5 = 16.291$, $P < 0.0001$	
Linepithema humile	20	9	0.460 ± 0.036	0.55 ± 0.16	3.18 ± 0.95	0.96 ± 0.06	$t_8 = 6.740$, $P < 0.0001$	
	30	6	0.424 ± 0.008	0.66 ± 0.09	3.85 ± 0.53	1.79 ± 0.03	$t_5 = 9.424$, $P = 0.0002$	1.73
	40	6	0.428 ± 0.020	1.54 ± 0.07	8.96 ± 0.96	3.60 ± 0.14	$t_5 = 13.178$, $P < 0.0001$	
Crematogaster californica	20	5	1.435 ± 0.161	0.79 ± 0.08	4.63 ± 1.02	2.53 ± 0.24	$t_4 = 5.609$, $P = 0.0050$	
	30	7	1.360 ± 0.198	1.47 ± 0.38	8.57 ± 2.23	4.83 ± 0.60	$t_6 = 4.692$, $P = 0.0034$	1.82
	40	5	1.485 ± 0.209	2.66 ± 0.43	15.55 ± 2.53	10.43 ± 1.26	$t_4 = 5.940$, $P = 0.0040$	
Dorymyrmex insanus	20	5	0.613 ± 0.083	0.33 ± 0.02	1.91 ± 0.15	1.22 ± 0.14	$t_4 = 10.019$, $P = 0.0006$	
	30	6	0.579 ± 0.025	0.67 ± 0.06	3.94 ± 0.37	2.33 ± 0.09	$t_5 = 8.964$, $P = 0.0003$	2.25
	40	6	0.571 ± 0.046	1.57 ± 0.27	9.16 ± 1.55	4.60 ± 0.32	$t_5 = 7.036$, $P = 0.0009$	
Solenopsis xyloni	20	5	0.415 ± 0.023	0.32 ± 0.06	1.86 ± 0.37	0.88 ± 0.04	$t_4 = 6.009$, $P = 0.0039$	
	30	6	0.431 ± 0.012	0.76 ± 0.09	4.42 ± 0.51	1.81 ± 0.04	$t_5 = 13.094$, $P < 0.0001$	1.78
	40	6	0.648 ± 0.096	1.47 ± 0.15	8.56 ± 0.85	5.13 ± 0.66	$t_5 = 18.624$, $P < 0.0001$	

Data are reported as mean ± SD. N = sample size. MR = metabolic rate. SMR = standard metabolic rate predicted by the allometric equation for inactive tracheate arthropods, using a $Q_{10} = 2$ (Lighton et al., 2001).

(Lighton, 1994, 1998). However, we can speculate that RWL is a small component of total water loss just because it is under strong natural selection. This has been only partially demonstrated as changes of gas exchange patterns resulting from selection (Gibbs, 1999) for desiccation resistance in *Drosophila* in the laboratory (Williams et al., 1997, 1998). Selection to reduce RWL is also supported by the fine control of spiracle opening even under highly energetic activities such as flying (Lehmann, 2001). The two main pathways of water loss in insects, i.e., through the cuticle and the spiracles, may both have been minimized by natural selection, but the selective mechanisms evolved independently because mechanisms to reduce water loss are completely different in each case. To reduce water loss through the cuticle the thickness or the composition of waxes and other hydrocarbons can be modulated, while to reduce water loss through the spiracles the morphology of the spiracles may be altered or their degree of opening kept to the minimum that is strictly necessary to exchange gases, i.e., CO$_2$ and O$_2$, without imposing a needless RWL penalty (e.g., Lehmann, 2001).

It has been widely suggested that the DGC evolved to reduce RWL, although other possible explanations have recently been discussed (see Bradley, 2000; Hetz and Bradley, 2005; Lighton, 1996; Lighton and Berrigan, 1995; and also Chown et al., 2005 for review). Only a few comparative studies concentrate on the importance of RWL (e.g., Chown and Davis, 2003), but RWL in insects that show a pattern of continuous gas exchange remain largely uninvestigated. This is not because RWL is thought to be unimportant in insects with continuous gas exchange, but until now distinguishing between cuticular and spiracular water loss rates (WLRs) in insects with continuous gas exchange was technically not feasible (but see Gibbs and Johnson, 2004; Lighton et al., 2004). The hyperoxic switch (Lighton et al., 2004) is a non-invasive technique that modulates spiracular opening by manipulating gas composition, and permits the measurement of RWL in insects with continuous gas exchange. This technique has the advantage that it can be used for groups of insects. This, in turn, allows investigators to improve the signal/noise ratio when making measurements of WLRs in insects, ants in this case, with a mass of an order of magnitude smaller than has been measured by open flow respirometry, with the concomitant advantages of this methodology, i.e., the high temporal resolution, which allows minimization of measurement errors and overestimates (for discussion see Lighton and Fielden, 1996; Lighton et al., 2004).

In this study we measured physiological characteristics of insect gas exchange such as metabolic rate, cuticular permeability (CP), RWL and maximal rates of RWL through diffusion (which could be an indicator of total respiratory throughput capacity) in groups of insects exhibiting continuous patterns of gas exchange. To measure these parameters we applied recently developed methodologies to measure RWL in insects with continuous gas exchange, i.e., the hyperoxic switch method (Lighton et al., 2004), and the correlation between water-loss and CO$_2$ emission rates (Gibbs and Johnson, 2004). We also compared these two