Notes from Underground: Towards Ultimate Hypotheses of Cyclic, Discontinuous Gas-Exchange in Tracheate Arthropods[1]

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SYNOPSIS. The Discontinuous Gas-exchange Cycle or DGC is generally thought to have evolved primarily as a means of reducing respiratory water loss rates in tracheate arthropods. However, several lines of evidence suggest that this supposition is oversimplified. I suggest that the DGC originated as an adaptation to the hypoxic and hypercapnic environments characteristic of underground burrows, rather than *primarily* as an adaptation to reduce respiratory water loss rates. This suggestion is based on a consideration of trans-spiracular oxygen and carbon dioxide partial pressure gradients in such environments, and the concomitant importance of decoupling oxygen and carbon dioxide exchange. The occurrence and/or absence of the DGC in sundry arthropod taxa is discussed, and diverse phylogenetic and other arguments are advanced for the inferred distribution thereof.

Confronted with a strange and undescribed phenomenon, particularly one as dramatic as the periodic outbursts of CO_2 from lepidopteran pupae described by early workers in insect respiration and now referred to as Discontinuous Gas-exchange Cycles or DGCs (see reviews referenced by Lighton, 1996), one's search for feasible evolutionary or ultimate explanations is naturally circumscribed by one's scientific world-view. If that world-view was formed in large part by classical investigations into insect water-balance, many carried out in the 1930s to 1970s (see Edney, 1977 for an overview of the field), then ultimate explanations of the DGC based on water balance considerations will have presented themselves with urgency, clarity and consistency. What could be more logical? It had long been known (see review by Kaars, 1981) that inducing spiracular valves to open fully greatly exacerbated respiratory water loss rates. From this it follows that the natural diminution of those rates must invoke stringent strategies of spiracular control. Relative to artificial hypercapnic induction of

spiracular opening the DGC simply seemed the *reductio ad absurdum*, the opposite end of the spiracular-control continuum, at which water loss rates were depressed to an irreducible minimum because spiracular openings were likewise at a minimum consistent with maintenance of mitochondrial respiration. And none could argue that if one quested for an animal system with minimal latitude for water loss, the immobile pupa stoically re-coding its ontology underground was surely the grail.

Faced with an ultimate explanation so well in accord with the facts, the most important questions of proximate mechanism proved straightforward to answer (see reviews referenced by Lighton, 1996), especially because large immobile pupae are the most tractable of research animals. After the 1970s further work in the field was minimal. After all, by that time both ultimate and proximate explanations of the DGC were neatly squared away and accessible to anyone possessing a university library card. And as is well known today, further research in an already established field is often condemned as mere matrix-filling (Feder *et al.*, 1987).

When quantitative research on the DGC of adult insects was finally undertaken in the 1980s and 1990s independently by Kestler, Lighton, Harrison and others, evidence rapidly accumulated suggesting that the ini-

tiation and termination of each of the DGC's three phases, as defined in the pioneering work of Howard Schneiderman and others, were similarly determined in lepidopteran pupae and in adult insects (review by Lighton, 1996). Aspects of this research are still in progress (Lighton and Garrigan, 1995; Krolikowski and Harrison, 1996; JRBL and B. Joos, in preparation) and will not be treated in detail here; readers unfamiliar with the basics of the DGC are referred to Lighton (1996) and reviews cited in that paper. Much of the impetus for undertaking this proximate-mechanism research lay in the serendipitous discovery that cockroaches (in the case of Kestler) and certain tenebrionid beetles and practically all ants (Lighton) exhibit pronounced and predictable DGCs. Even more helpful, in the case of ants, decapitation had little effect on gas exchange control. Invasive protocols, which were otherwise out of the question because of their effect on behavior and thus on the DGC, could therefore be used to explore proximate mechanisms further (e.g., Lighton, et al., 1993b; Lighton and Garrigan, 1995).

My intent here is not to outline past and present research concerning the proximate mechanisms of the DGC, interesting though those mechanisms are. Rather, I want to step back from mechanism and concentrate on the why's rather than the how's of the DGC. Implicit in the term "serendipitous" above is the fact that not all adult insects display a stereotyped DGC or even a DGC of any recognizable sort. Human psychology, in its love of patterns and of irregularly shaped pieces of existence which through suitably ingenious topological manipulations can be fitted to existing patterns, for the most part comfortably ignores the uninterpretable. Thus numerous non-Popperian, stochastic and even opportunistic investigations of insect gas exchange that took place while exploring its extent and characteristics have gone unpublished because the relevant insects appeared grossly ignorant of the literature, or in other words yielded data uninterpretable under the current DGC paradigm.

For example, just as I cannot further your understanding of the hygric correlates of

the DGC by mentioning that I am writing this paper on a beautiful mid-March day in a research vehicle on a playa in the east Mojave Desert, nor can I do so by mentioning that the successful xeric beetle genus Eleodes does not, on all available evidence, employ a DGC. The first statement belongs to a narrative, while the second is an example of the reporting of negative results—a practice more honored in the breach than the observance, and for good reason. The latter statement implies that the author lacked the patience or skill to induce Eleodes to behave "normally" in the measurement regime, or—worse—that Eleodes does in fact exhibit a DGC of a sort too subtle or complex for the author to recognize or analyze. If incremental contributions to our understanding are rightly regarded as "signal" while awkward observations such as Eleodes' heterodox gas-exchange characteristics—awkward because they are not connected to a recognized conceptual framework—can be regarded as "noise", our publication system constitutes a noise filter par excellence. If it is strong enough, the noise may overwhelm the signal and a Kuhnian paradigm shift may occur. Weaker noise may remain in the background for decades.

There is a lot of noise in the background of the DGC. This is not to deny the DGC's validity in the arthropods that employ it—all ants, for example, and some roaches, orthopterans, beetles, and non-insect tracheate arthropods, not to mention diapausing lepidopteran pupae. But speaking as someone who has examined more insects in flow-through respirometry systems than anyone else to my knowledge, readily interpretable DGCs are the exception rather than the rule. You would never guess this from my papers or those of my colleagues. There is no cover-up, no conspiracy; merely the fact that the goal of the publication process is that papers should contain the imperishable ingot of truth from which the dross has burned away. The dross is the exception that proves the rule, the negative result, all things (in Gerard Hopkins' words) counter, original, spare and strange; all constitute the noise that contaminates the signal. Thus the last generation of physiologists placed great

emphasis on extracting mean values for physiological parameters from noise's booming, buzzing confusion. By so emphasizing means they ignored the noise-borne signals of inter-individual variability on which evolution, of course, depends (see *passim* Feder *et al.*, 1987). There was nothing wrong with their methodology at the time because elucidating mean-ing was a vital step in the conceptual development of physiology. The elucidation of mean-ing is equally important for ongoing research into the proximate mechanisms of the DGC. Paying attention to noise, however, constitutes generational learning and can deepen one's understanding of the blurred edge of proximate mechanisms—or, if you will, of the synchronically inferable trajectory of a physiological system through the diachronic adaptive landscape.

At the moment we can only pay lip service to listening for a signal in the noise of insect ventilation. I can cite no broad-ranging comparative studies of the dynamics of gas exchange in motionless insects that are simply being insects rather than doing something catering to our $\log_2(P)$-based intelligence such as walking, flying, mating, foraging or singing. The studies do not exist because no-one has had the time or personnel to make them and because such studies are labeled as mere matrix-filling by the leaner, meaner ethos of modern evolutionary physiology which is vertebrate-biased and lacks appreciation of the sumptuous depths of the arthropod evolutionary radiation. Evidence in support of my contention that the DGC is not universal or even particularly common among adult insects is therefore inferential and circumstantial.

Among published studies, some authors (Farrelly *et al.*, 1995) assume that the DGC is universal and operates exactly in accord with the models proposed by Schneiderman and others (see reviews cited in Lighton, 1996) in spite of recent studies that directly contradict them with respect to the relative importance of diffusion and convection in the DGC of adult insects (see Lighton, 1996 for review). Others assume that because the DGC "is" an adaptation to reduce respiratory water loss, it follows as the night the day that their study insect, being xeric, must

necessarily display the DGC (Ahearn, 1970; Loudon, 1989, to cite just two examples). In such a way two insects that never display a DGC (*Eleodes* and *Tenebrio*; JRBL, unpublished data) are established in the scientific literature as masters of the DGC (above citations, *inter alia*). The scattered examples of actual research on dynamic processes in *Tenebrio*, especially pupal (e.g. Slama *et al.*, 1979; Kuusik *et al.*, 1994 and references therein), are clever descriptive papers that alas are opaque in terms of underlying mechanisms, making their meaningful interpretation difficult. My own studies, which to my discredit are unpublished, confirm that gas exchange in larval, pupal and adult *Tenebrio* is complex and intermittently convective (see Lighton, 1996), as is the case with *Eleodes*.

In other insects, I have found no evidence for the DGC in dipterans (excepting xeric asylids; JRBL and F. D. Duncan, unpublished data), surface-dwelling tenebrionids (except *Cryptoglossa*; JRBL and B. Joos, unpublished data), hemipterans or homopterans (JRBL, unpublished data; one hopes that the relevance of the first few paragraphs of this MS is becoming clear). The DGC appears to be widely distributed in hymenopterans including all ants so far investigated (at least in the case of the alate castes); see Lighton (1996) for references, honeybees (Lighton and Lovegrove, 1990), bumblebees (JRBL, B. Joos, and B. Lovegrove, unpublished data), mutillids (F. D. Duncan and JRBL, unpublished data) and mud-daubers such as *Sceliphron* (JRBL and F. D. Duncan, unpublished data). The DGC generally occurs in psammophilous beetles (*e.g., Onymacris* spp; Lighton, 1991) and fossorial beetles (Carabids; JRBL, unpublished data; K. Slama, personal communication). It occurs in dictyopterans, though often only at low temperatures or after long periods of motionlessness (Kestler 1978, 1980, 1985), and it occurs unpredictably in adult orthoptera such as *Locusta* (JRBL, unpublished data) and grasshoppers (Hadley and Quinlan, 1993; Gulinson and Harrison, 1996; Krolikowski and Harrison, 1996). Apart from insects, tracheate arthropods that are known to exhibit a DGC include solphugids (Lighton and Fielden, 1996),

ticks (Lighton *et al.*, 1993*a*) but probably not other mites (Lighton and Duncan, 1995); pseudoscorpions (JRBL and B. Joos, unpublished data; K. Slama, personal communication) but probably not harvestpeople (JRBL and B. Joos, unpublished data). The gas exchange characteristics of Ricinuleids are completely unknown.

We have little to go on but combined with some elementary logic and a couple of permissibly bold extrapolations, the little we know can be used effectively. A pattern does emerge, though it is far from clear. With the chief exception of ticks, the DGC is common among tracheate arthropods that are likely to undergo periods of fossorial or claustral existence for at least part of their life-cycles. The DGC is uncommon, unpredictably and capriciously present, or altogether absent among arthropods that are not predictably subjected to potentially hypoxic or hypercapnic environments.

Let us put the ticks aside for the moment and summarize the biophysical parameters of the DGC *vs.* continuous gas exchange that may be relevant to our observed distribution.

The biophysical essence of the DGC is the decoupling of CO_2 emission from O_2 uptake, with the former occurring at high rates once per DGC and the latter occurring at low rates through most of the DGC (Lighton, 1996). Gas exchange may be purely diffusive (*e.g.*, in ants; Lighton and Garrigan, 1995 and JRBL and B. Joos, unpublished data) or may incorporate a convective component (*e.g.*, in beetles; Lighton, Bartholomew *et al.*, 1985; Lighton, 1991; JRBL and B. Joos, unpublished data). The ultimate game plan is to maintain adequate oxygen flux to meet mitochondrial requirements during inactivity, while releasing CO_2 as rapidly and infrequently as possible, because it is during CO_2 release that transspiracular water loss rates are highest (Lighton *et al.*, 1993*c*). In continuous diffusion-driven gas exchange, in contrast, O_2 uptake and CO_2 emission must be coupled and each must occur at equilibrium flux rates equal to the sum of the organism's mitochondrial gas exchange rates. The very different transspiracular partial pressure gradients for O_2 and CO_2 in normoxic/nor-

mocapnic environments (see below) dictate that "continuous" gas exchange will generally be intermittent and convective in nature.

We will now compare and contrast the DGC and continuous gas exchange in more detail, culminating with respiratory water loss correlates. We will use ants as our primary example animals because their DGC is the most thoroughly characterized of all adult insects.

NORMOXIC/NORMOCAPNIC GAS EXCHANGE

In the DGC, no significant external gas exchange takes place during the C or Closed-spiracle phase. During the F or Fluttering-spiracle phase of the DGC, O_2 enters the ant at a rate sufficient for mitochondrial respiration, closely controlled by modulating spiracular conductance to maintain a large trans-spiracular O_2 partial pressure (ΔP_{O_2}) gradient. Note that although many people assume that bulk flow of air down a putative transspiracular pressure gradient is important during the F phase in adult insects (Kestler, 1985; see especially Farrelly *et al.*, 1995), a non-Platonic approach to science demonstrates that such effects are minimal and insignificant (discussed by Lighton, 1996).

Taking a 10 mg ant with a metabolic rate of 18.1 μW or a fat-based V_{O_2} of 3.27 μl hr^{-1}, and assuming an ambient P_{O_2} of 21 kPa and an endotracheal P_{O_2} of 4 kPa (Lighton and Garrigan, 1995), effective spiracular conductance for O_2 during the F phase is about 0.19 μl hr^{-1} kPa^{-1}. Assuming a typical F phase RER of approximately 0.2, which has been experimentally verified in ants (Lighton, 1996 and references therein), and assuming an ambient P_{CO_2} of 0 kPa and an endotracheal P_{CO_2} of 4 kPa (JRBL and B. Joos, unpublished data), its effective spiracular conductance for CO_2 during its F phase is about 0.16 μl hr^{-1} kPa^{-1}, which is similar. Plainly, because of the very different partial pressure gradients for CO_2 and O_2, temporal separation of respiratory phases optimized for exchange of each gas species must occur unless we hypothesize that Maxwell's demon haunts the spiracles of tracheate arthropods and orchestrates a gas-dependent modulation of spiracular

conductance—which is doubtful, as we have just seen. This explains the requirement for the O or Open-spiracle phase, during which accumulated CO_2 is released, unfortunately with a large accompanying loss of water vapor.

Truly continuous gas exchange requires the continuous emission of CO_2 at the rate VCO_2, and uptake of O_2 at the rate VO_2. In a diffusion-driven regime, spiracular conductance for CO_2 and O_2 must therefore be approximately equal. If endotracheal P_{CO_2} is maintained at about 4 kPa, endotracheal P_{O_2} must therefore stabilize at approximately 17 kPa (a four-fold lower ΔP_{O_2} than in the case of the DGC F phase). In other words, spiracular conductance must increase roughly four-fold relative to the F phase of the DGC in the case of diffusion-driven continuous gas exchange. And unfortunately, transspiracular water flux rates must increase by a slightly more than proportionate amount in view of the high diffusivity of water vapor.

We can therefore conclude that continuous, diffusion-driven gas exchange is not a viable strategy except in water-saturated air. This conclusion is supported by the observation that the spiracles of certain small hygric arthropods, such as collembolans, have minimal or absent control capability. In the case of insects exposed to xeric conditions, it is obvious from first principles that continuous gas exchange must, where it occurs, be intermittently convective. Furthermore, it is obvious that in order for the volumes of CO_2 and O_2 exchanged to be approximately equal in each convective event, the transspiracular partial pressure gradients for CO_2 and O_2 must be equal. A given volume of convective gas exchange will thus release and deliver a given volume of CO_2 and O_2, respectively, allowing of course for the RQ of the animal. If this is not the case—for example, if CO_2 is allowed to accumulate—then occasional bouts of more rapid ventilation designed specifically for the enhanced release of CO_2 must occur. If so, the intermittent-convective gas exchange regime begins to approach the DGC, with diffusion replaced by convection. This is exactly what we observe in psammophilous beetles (Lighton, 1991)

whose status as "true" DGC-exhibiting animals could accordingly be questioned, although their gas exchange dynamics are functionally equivalent to the DGC type (see below). If, on the other hand, the volumes of CO_2 and O_2 that are exchanged in each convective bout are equal, we arrive at the apparently continuous gas exchange of Eleodes and Tenebrio. And if each convective bout takes place before the air within the outer reaches of the tracheal system has become fully saturated with water vapor that has evaporated from the tracheoles, the intermittent-convective regime could actually reduce overall water loss rates relative to the DGC with its water-profligate O phase. Recall that during the O phase of the DGC, continuous diffusion of water vapor occurs from the tracheoles to the external atmosphere. Empirical studies have confirmed that when this occurs, water vapor is lost at the predicted molar ratio relative to CO_2 (Lighton and Garrigan, 1995).

The opportunities to test our understanding of intermittent-convective systems by manipulating ambient gas mixtures are obviously legion, but are not further explored here. Rather, we note that continuously intermittent-convective systems must, by their nature, be highly sensitive to deviations from ambient CO_2 and O_2 partial pressures. One could stress such a system by placing it in an underground or chthonic environment, for example, where the gas exchange demands of the animal itself plus extensive microbial activity conspire to create severe hypoxia and hypercapnia. With each ventilation event, the animal at first may actually gain CO_2 and lose O_2—hardly a helpful scenario. In order to gain sufficient O_2 and lose sufficient CO_2, the animal would have to increase its ventilation rates and/or volumes to an extent that could be highly detrimental to its water balance (assuming imperfect water vapor saturation in its surroundings), and that may have implications for its pH regulation as well.

In contrast, the diffusion-based DGC is a functional and viable gas exchange strategy in hypercapnic and hypoxic environments. The DGC's decoupling of O_2 uptake and CO_2 emission has several major adaptive advantages. A partial list would include:

● The endotracheal P_{O_2} of about 4 kPa during the F phase allows inward diffusion of O_2 even at low ambient P_{O_2}.

● The presence of a C phase, during which external gas exchange is negligible, facilitates the diffusion of O_2 to areas adjacent to the insect prior to the F phase and mitigates the dilution of available O_2 resources by CO_2 emitted during the previous O phase.

● The marginal emission of CO_2 during the C and F phases facilitates the diffusion away from the insect of CO_2 emitted during the previous O phase, expediting the later outward diffusion of CO_2 during the O phase.

● The sequestering of CO_2 within the ant until the initiation of the O phase facilitates the formation of the largest possible CO_2 partial pressure gradient for the rapid outward diffusion of CO_2.

● In practice, the high water loss rate during the O phase could be mitigated by the relatively high ambient water vapor pressure in most underground environments.

In other words, an argument can be made that the genesis of the DGC is not purely hygric (based purely on water conservation) but is at least partly chthonic (based on the peculiar challenges of gas exchange in a hypoxic/hypercapnic environment); see also Lighton (1996). This hypothesis is supported by the fact that the majority of arthropod species exhibiting a DGC either periodically inhabit, or at some point of their adult life are selectively bottlenecked by, hypoxic and/or hypercapnic environments. It is worth emphasizing that this argument emphatically applies to diapausing lepidopteran pupae (the "classic" DGC system) as well as to adult insects; recall that such pupae in nature are typically buried at a significant depth in the soil.

Given the possibility that the ultimate evolutionary pressures behind the DGC may not have been primarily hygric but rather chthonic, what are the advantages of more continuous gas-exchange, such as in the intermittent-convective or IC regime mentioned above? A partial list may include:

● Greater constancy of the insect's internal environment, especially in terms of proton balance.

● Ease of transition from inactive to active metabolism, which disrupts the DGC (Lighton, 1988) but would merely alter the volume and frequency of an IC cycle.

● Potentially lower water loss rates, provided:

(a) Air expelled from the insect during each IC event is not fully saturated with water vapor, and/or

(b) Air admitted during each IC event is enriched in water vapor, for example by the subelytral chamber of many beetles which is continuous with the abdominal spiracles, and which offers a way to mitigate respiratory water loss rates by offsetting them against an insensible integumentary water loss component, which in turn can be reduced by the respiratory water loss component, and/or

(c) Strategic use is made of pressure cycles of the sort described by Corbet (1988), which (if properly timed) may subsaturate the excurrent air from each IC event, and/or

(d) The endotracheal air is maintained in a subsaturated state by active uptake of water vapor, for example by maintaining a strongly hyperosmotic endotracheal reservoir from which water can be extracted in the manner of ticks (external) and perhaps Tenebrio larvae (partly internal); reviewed by Hadley (1994).

We now consider two series of studies that have yielded data relevant to the above lines of reasoning (see also Lighton, 1996).

First, the female workers of ant colonies can be considered for many practical purposes as genetically identical, having a relatedness coefficient of 0.75 (in most colonies) rather than the 0.50 common among sibs of other sexually reproducing organisms. This leads to an interesting paradox. Relative to the worker ant herself producing offspring, a greater proportion of a worker ant's genes can be instantiated by ensuring that the queen ant produces more offspring in the form of worker ant sisters. This is

because any worker-ant offspring will have a relatedness coefficient of only 0.50, rather than 0.75, relative to the worker, who in any event is usually sterile (see Hölldobler and Wilson, 1990). It is a truism in ant biology that worker and queen ants have very different colony-level agendas (above citation). These differences, together with other differences in behavior, environmental exposure and the like, result in very different colony-level selective pressures operating on workers and queens. Workers are thus generally behaviorally, physiologically and morphologically quite distinct from queens in spite of their intricately entangled common genetic heritage.

Significantly, queen ants experience gas exchange challenges that may be substantially different from those experienced by their worker ants. Most queen ants found colonies by entering a solitary claustral stage during which they fast within a sealed underground chamber. Such chambers are likely to become hypoxic and hypercapnic. The solitary queen lays eggs, feeds and raises larvae, and finally allows the resulting diminutive first brood of workers to leave the nest and forage. Once the colony is thriving, the nest is generally well-ventilated and workers may spend a significant proportion of their time foraging in the normoxic/normocapnic but desiccating external environment while the queen remains in the deepest strata of the nest (see Hölldobler and Wilson, 1990).

In a recent study, David Berrigan and I hypothesized that the harvester ant *Messor pergandei* may, in view of the hyper-xeric nature of its Mojave Desert habitat, display gas exchange strategies that differed between workers and queens. It should be noted that the workers of *M. pergandei* form ordered foraging phalanxes up to a hundred meters long which expose workers to desiccating conditions for prolonged periods of time. Consideration of the radically different environments of workers and queens, together with observations of the "continuous" gas exchange characteristics of successful hyperxeric inhabitants such as *Eleodes,* prompted us to frame this differential, caste-linked gas exchange hypothesis.

In our study (Lighton and Berrigan,

1995) we found that female alates (putative queens) displayed the normal, three-phase DGC expected for ants, while the workers emitted CO_2 continuously and without significant variation. However in a very closely related, congeneric species (*M. julianus*) from a mesic environment the workers displayed normal DGCs. I am currently preparing to investigate the nature of gas exchange in *M. pergandei* workers. In any event, we now have an example of loss of the DGC in a caste subjected to more hygric and fewer chthonic stresses than those that challenge another caste *in the same species and same nest* that does exhibit a DGC. This evidence that the ultimate selective pressures leading to the development of the DGC were chthonic rather than hygric is suggestive, if not yet convincing. Further indirect evidence comes from the evolution among solphugids of a three-phase DGC practically identical to, though independently derived from, that of adult insects that display the DGC. It should be noted that solphugids, as fossorial animals, may often be exposed to hypoxic/hypercapnic conditions in deep, sealed underground burrows (JRBL, personal observation).

Finally, ticks may appear the exception to the above generalizations. They do not live in hypoxic or hypercapnic environments, and yet exhibit a pronounced diffusion-based DGC (Lighton *et al.,* 1993). While considering this apparent anomaly, the reader is invited to cogitate on the fact that well-hydrated lubber grasshoppers exhibit an apparent DGC while dehydrated lubbers—water-stressed lubbers—do not (Hadley and Quinlan, 1993). Furthermore, ticks that are water-stressed likewise show a disruption of their DGC (Fielden and Lighton, 1996) at exactly the time when the hygric DGC-genesis hypothesis predicts that the DGC would attain its most perfect expression.

To assemble these jigsaw pieces, consider that most ixodid ticks feed only once in their adult life, and that years may elapse between molting into an adult and consummating the tick lifestyle with a last (and first) supper as a fully mature bloodsucking parasite. Two crucial adaptations allow ticks to survive for this festive occasion.

First, they have unusually low metabolic rates, about 10% that of insects and spiders (Lighton and Fielden, 1995); and second, they can absorb water directly from subsaturated air and thus are seldom if ever in prolonged negative water balance in nature (Needham and Teel, 1986).

Next consider that because of the decoupling of O_2 and CO_2 exchange in the DGC, a great deal of CO_2 must be sequestered in the tissues and hemolymph without causing excessive pH swings prior to the O phase. If the hydration level of the animal is not adequate, then raising the animal's buffer concentrations (over the long term) to maintain tolerable swings of pH cannot proceed for long without causing intolerable osmotic stress. This explains the failure of dehydrated lubbers, and of dehydrated ticks, to sustain a DGC (Hadley and Quinlan, 1993; Fielden and Lighton, 1996). Ticks generally maintain positive water balance by active water vapor absorption (Needham and Teel, 1986), so water balance is not usually a problem and the tick DGC can be sustained indefinitely.

Why then bother to sustain a gas exchange strategy in ticks that may, as we are inferring from other evidence, be inferior to intermittent convection for an animal in a normoxic, xeric environment? The answer lies in the extraordinarily low metabolic rates of ticks and the fact that literally years may pass between molting and feeding (Lighton and Fielden, 1995). Ultimately, in such a stochastically opportunistic and stringently energy-limited animal, selection has favored a passive (diffusion-based) rather than active (convection-based) gas-exchange strategy in order to conserve somatic energy stores. This strategy is practical because the hydration level required to sustain the DGC is ensured by active water vapor uptake. Thus the case of ticks actually supports our main arguments about the selective correlates of the DGC, albeit in a devious way.

The DGC therefore probably (but not certainly) originated as an adaptation to the hypoxic and hypercapnic environments characteristic of underground burrows, rather than *primarily* as an adaptation to reduce respiratory water loss rates. We have seen

that this tentative conclusion is supported by several independent lines of evidence. It is also tempting to suggest here that the minimal impact of the K-T meteor on most terrestrial arthropods (relative to the catastrophic extinction of many vertebrate and molluscan taxa, both terrestrial and aquatic) may be explained by the relative tolerance for hypoxia and hypercapnia endowed by the DGC.

In conclusion, it is tempting to model many of the above verbally-presented ideas in explicitly mathematical form, but too many variables are as yet unknown or known with only the poorest accuracy to make such modeling a heuristically rather than delusionally useful exercise. Much more research is needed. Actively publishing workers in the field of arthropod gas exchange dynamics can currently be counted on the fingers of one hand, so the large unknown areas are easily explained. I look forward to the day when this rich and important field of research attracts the talented graduate students and postdoctoral fellows that it deserves.

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