With Reference to Invertebrate Examples, What is Life Like at Very Small Scales?

Invertebrates are characterised by lacking vertebras, a row of bones that extend down the back, and they consist of 97% of described animal species, the remaining 3% being the subphylum of Vertebrata. Invertebrates make up twenty-nine of the thirty phyla and they are even present in the one remaining phylum. Within the invertebrates reside arthropods in which the superclass Insecta exists *(Pearse V et al, 1987)*, and this essay will mainly explore what life is like at the scale of insects. The smallest of insect species are among the smallest metazoans, comparable in size even to some unicellular organisms. The smallest is thought to be the males in the wingless parisitoid species *Dicopomorpha echmepterygis*, which can be as small as 139µm. As species such as these get smaller, there is a general allometric trend of dramatic simplification of morphological structures, termed 'pumilistic degeneration' *(Polilov AA, 2015)*. Although these microinsects (insects with adult body sizes less that 2mm) are particularly tiny, all insect species are relatively small compared to humans and most other vertebrates, and therefore their systems and survival techniques must be highly specialised to the scales at which they live.

The Gas Exchange System

One of the major features of insects which relates to their size is the presence of a tracheal gas exchange system. Due to their reduced volume insects can somewhat rely more on simple diffusion to supply their cells with oxygen and eliminate carbon dioxide than larger animal species could. This means that there is more of a disparity between their circulatory and gas exchange system than there is in vertebrate species. The blood in vertebrates is used to deliver oxygen to and remove carbon dioxide from respiring muscles, whereas the haemolymph in insects rarely contains respiratory pigments and hence does not have an oxygen-carrying capacity *(Gullan PJ & Cranston PS, 2014)*. This is because the surface-area to volume ratio of smaller insects is much greater; therefore they can rely more on direct diffusion of oxygen to their tissues rather than using a liquid medium to deliver it around the body.

The respiratory system consists of tube-like cuticle-lined tracheae which branch throughout the body. These tracheae can exchange gases with the atmosphere through openings called spiracles; muscular controlled openings which are positioned laterally on the surface of insects. Within the system there are large tracheal trunks as well as distensible air sacs that act as reservoirs of air inside the body. The finest tips of the tracheae are termed tracheoles. These make contact with internal organs and are the primary site of gas exchange with the respiring tissues *(Bradley TJ, 2007)*.

Despite the fact the diminished size of insects allows them to rely on this form of a gas exchange system, there are further adaptive strategies found in some insects which makes the gas exchange more efficient. Gas exchange is not necessarily continuous and many species display cyclic or discontinuous respiration patterns. This means small insects have evolved a behavioural repetition based around a recurring pattern of change in their tracheal system known as discontinuous gas exchange cycles (DGCs). These start with a closed-spiracle phase where little or no gas can diffuse into or out of the system. This can occur due to the presence of valves surrounding the atrium of a spiracle *(Gullan PJ & Cranston PS, 2014)*. In this phase, cells are using oxygen up and thus the partial pressure of the gas within the body will drop. This is followed by a flutter-spiracle phase where the spiracles will repeatedly open and close. Due to the higher partial pressure of oxygen in the atmosphere, there will be an influx of the gas into the tracheal system. However, within this phase carbon dioxide will also partially build up within the body. The cycle is terminated by an open-spiracle phase when the waste carbon dioxide gas diffuses out. This cycle is important for overcoming a problem that can be experienced by invertebrates at this scale. Although their smaller size, and thus larger surface area to volume ratio, facilitates direct diffusion to tissues, it also causes high rates of water loss from the tracheal system. Therefore, DGCs exist to partially overcome this problem by reducing the rate of water efflux than if the spiracles were always open for free gas exchange *(Lighton JRB, 1996)*.

As well as the presence of these DGCs, some species of insects can mechanically alter the volume of their body to essentially ventilate their tissues actively. This is often observed in larger more active insects that require efficient gas exchange to deliver oxygen to respiring muscles. The abdomen rhythmically pulses due to changes in internal body pressure (haemocoelic, intratracheal or haemolymph pressure). This change in pressure acts on the walls of tracheal sacs and tubes, thus causing bulk-flow of the gases through spiracles *(Sláma K, 1998)*.

In the smallest insect species, the tracheal system is much more reduced. In the majority of microinsects, only longitudinal stems are present with very few branching trachea and in some cases the gas exchange will only take place through a single pair of tracheae *(Polilov AA, 2015)*. In these species, mechanical ventilation will definitely not take place and the distance at which oxygen must diffuse is relatively small.

The way in which oxygen is delivered to respiring muscles in these invertebrates is directly linked to flight, one of the major evolutionary successes present in some species of insects. Flight is adaptively significant as it allows animals to take more direct routes, travel at higher speeds and avoid terrestrial predators. Flight in insects is driven by the levering motion of hind and fore wings which produce lift. These are moved under the control of dorsoventral muscles which when contracted pull down on the tergal plate and lever up the wing on the pleural pivot *(Brackenbury JH, 1992)*. The regular and repeated contractions of these muscles during flight are much more energy demanding than other forms of locomotion observed in animals and thus oxygen delivery to respiring tissues must be highly efficient. In evolutionary terms, insects have avoided investment in extensive circulatory systems but instead exploit their size such that oxygen from the environment can diffuse directly to respiring muscles, increasing efficiency *(Lighton JRB, 1996)*.

An insect's small scale has a direct link to its respiratory and gas exchange system, a constituent morphological and physiological feature which is integral to what life is like for any animal species. Their small size makes it possible to have a gas exchange system based on direct diffusion of oxygen to respiring tissues. This leads to the potential for aerobic metabolic performance that far exceeds vertebrate limits, including flight, a central characteristic of the lives of many insect species *(Lighton JRB, 1996)*. However, the fact insects depend on this tracheal system to deliver oxygen around the body puts an upper limit on the size to which they can grow to in evolutionary terms. The design of the system means that if oxygen must diffuse over considerable distances, the respiratory requirements of a large and active insect either could not be met, or would result in a significantly substantial loss of water vapour through their spiracles *(Gullan PJ & Cranston PS, 2014)*. This demonstrates how the gas exchange system in insects relates to the scale at which they exist and how it affects their lives because of their diminished size.

Gravity and Forces Within Water

The small scale at which insects live has particular connotations with regard to the forces that they may experience. This can be seen in both in the cohesive and adhesive force of water as well as the force of gravity and air resistance.

Because of their reduced size, insects are in less danger of putting themselves at risk by falling from tall heights. The resistance enforced to movement of a falling entity by air is proportional to the surface area of the thing that is moving. If the dimensions of an animals three dimensional shape (its length, breadth and height) are divided by ten, its weight is reduced to a thousandth but the surface area is reduced to a hundredth (assuming both individuals have the same density). This means that the resistance experienced by the smaller individual is relatively ten times greater than the falling gravitational force *(Haldane JBS, 1926)*. Relating this to small insects, it means that life for insects is unlikely to be impeached by gravitational forces in any way as they impose little danger upon them.

However, a force which is much more endangering for a small terrestrial insect is that of water adhesion and cohesion, which leads to surface tension. In his paper, Haldane wrote, *"an insect going for a drink is in a great danger as man leaning out over a precipice in search of food" (Haldane JBS, 1926)*. This is because if an insect is submerged in water, on resurfacing it will be carrying many times its own body weight in water. This could damage or interfere with the respiratory system of non-aquatic insects or simply immobilize the organism thus endangering it. This occurs because of the presence of hydrogen bonds in the water. These mean that not only will the polarized water molecules 'stick' to an exposed surface, such as the body of an insect, but they will also drag other water molecules out by its cohesive force *(Alberts et al, 2015)*. This demonstrates how the adhesive and cohesive forces in water can endanger invertebrates because of the disproportionate effect it has on organisms living at a small scale.

Despite the danger these forces pose on insects, they are in some cases exploited by insects, made only possible because of their diminished size and weight. Some species have evolved the ability to secrete 'light oil' and harness the water-like attributes of this secretion to enable climbing on smooth surfaces at $90^{o}<$ angles *(Walker G, 1993)*. Blowflies release this non-volatile liquid onto the spatulate ends of their tenet hairs. The surface tension of this lipid secretion underneath the hairs is sufficient to propagate successful adhesion of the individuals to smooth surfaces *(Walker G, Yulf AB & Ratcliff J, 1985)*. Although the production of these secretions are integral to this behavioural process, it would not be possible without the insects existing as extremely small and lightweight organisms. As well as exploiting their light weights' and the surface tension of water in their physiology, some insect species use them as a habitat within the environment. The surface tension of water is a sufficiently strong force that it can act as static weight support for some species such as those found in the family *Gerridae*, commonly known as pond skaters. These species can propel themselves on top of the water by driving their central pair of hydrophobic legs in a 'sculling' motion *(Hu DL, Chan B & Bush JWM, 2003)*.

The effect that these different forces can have on small insects because of their size alters the way in which insects survive and interact with their environment. The effects of the forces can be either exploited to aid the invertebrate's survival, or it may pose a danger to the organism and hinder its chances of survival. In both cases, the reason for it is directly linked to the size and small scale at which they live.

Predation

Something directly related to the small size of insects, as well as most likely being related to the extreme abundance of species and individuals, is the fact that they are readily preyed upon. That is to say that their diminished size, in comparison to many other members in the animal kingdom, means that they are physically small enough to be commonly preyed upon. They are subject to predation by other arthropods, as well as insectivorous and omnivorous vertebrates such as fish, birds and small mammals *(Speight MR, Hunter MD & Watt AD, 2008)*.

This high rate of prey-predator interactions has resulted in a huge diversity in defensive methods that can be observed in insects. This includes camouflage and mimesis in their natural environment, mimicry of other species, mechanical defenses, chemical defenses and collective defenses in gregarious insects *(Gullan PJ & Cranston PS, 2014)*. Although it would not be valid to say these evolved solely because of the scale at which insects live, it is likely that the reduced size provided an extra evolutionary force to protect from the high diversity and sheer number of predators.

Conclusion

The small scale in which they live vastly affects the life and survival of insects. The scale to an extent determines the way in which vital physiological systems exist within their bodies and their behavioural traits from both an individual organism's and an evolutionary standpoint. This essay has focused primarily on insects as an example of invertebrates that live at small scales. It should be clarified that this means that many of the discussed features may be specific to the Insecta class and not to all invertebrates. However, all invertebrates that live at small scales have to manage with a different set of niches to fill and survival hindrances to overcome than there are with larger vertebrates. This radically alters what life is like for invertebrate species which live at smaller scales.

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