

Overview: extreme environments

R. C. TINSLEY

Bristol University

INTRODUCTION

An important element in most approaches to the subject of parasitism is the consideration of environment. Parasites are set apart within animal ecology because they experience two environments, one the 'external' conditions and the other created by the living body of the host. As in any ecological system, external environmental conditions have a major influence on life history parameters: these conditions may be experienced directly by 'off-host' stages of a parasite or, to a greater or lesser extent, indirectly through the body of the host. However, uniquely in parasitic associations, the internal (host) environment has a dual influence on the physiological conditions encountered by parasites: first, the host buffers the external conditions (by homeostatic mechanisms moderating environmental fluctuations, by behavioural responses selecting appropriate habitat conditions, etc.), but second, the host creates a suite of hostile factors associated with immune defence. This living, reactive environment has no parallels elsewhere in free-living animal ecology: it has the characteristic of reacting specifically to kill the organisms within its boundaries.

The approach of this supplement is to examine environmental constraints affecting parasites at four levels. First, there is a focus on selected physical (abiotic) conditions that are hostile to life in general and a review of the specific adaptations that allow survival of highly specialized parasites. Second, particular macro-environments (ecosystem conditions) are considered in which a series of environmental factors may combine to jeopardize survival, for instance in deserts and the deep-sea. Third, there is a detailed examination of certain micro-environments (host conditions) which may not at first sight appear limiting but which actually present a major challenge to parasite exploitation (the skin of fishes, the lungs of tetrapods). Finally, this volume considers the outcome of constraints over an evolutionary timescale, including the concepts of the niche, the arms race and host immunity, adaptation, specificity and host-switching, and inferences from phylogeny.

Extreme environments

Major constraints are easily recognized where environmental conditions approach the limits at which

life can be sustained. These conditions may be regarded intuitively as 'extreme'. However, the concept of an 'extreme environment' may be criticized as anthropocentric. Clearly, whilst specific conditions may exclude survival by a majority of animal groups, animals living in supposedly extreme environments appear to behave as if they regard their environment as 'normal'. Animals inhabiting the deep-sea (see Bray *et al.*, this supplement) illustrate the difficulty of defining conditions as 'extreme' and 'normal'. When removed from the high pressures and other constraints of their 'extreme environment' and brought to the surface, these animals are rapidly killed. Emperor penguins not only survive the Antarctic midwinter exposed to blizzards and to temperatures of -50°C , they also incubate their eggs during this period and endure over 3 months without feeding. Of course, this life style is 'normal', the product of a long process of evolutionary adaptation. If this view of 'extreme environments' is anthropocentric then it reflects an obvious fascination for both the scientist and layman. Perhaps the greater feat of endurance was that undertaken by the humans – a species singularly poorly-adapted to these conditions – who first undertook a midwinter expedition, subsequently called 'The worst journey in the world', in order to collect Emperor penguin eggs for studies concerned with development and evolution (Cherry-Garrard, 1922). For this species, the conditions are indisputably 'extreme'.

In the field of human endeavour, the concept of 'extreme' is often measured in terms of the proportion of attempts that fail. The highest levels of severity are reserved for cases where only a small minority of individuals, those exceptionally capable, succeed in a particular venture. Indeed, this may lead to the eulogizing of 'heroic failure' (as in the early exploration of polar regions). The popular view of extreme conditions evokes a significant degree of 'suffering' (ranging from discomfort to life-threatening dysfunction). In nature, of course, failures would not be a routine occurrence and it is unlikely that animals adapted to severe environmental conditions experience 'suffering': the conditions are 'normal' to them. For many biologists, the concept 'extreme' relates to physical and other environmental conditions where most life is excluded but some groups of organisms may routinely tolerate these conditions as a result of specific adaptations. Thus, the anthropocentric view may perhaps be

distinguished by its focus on the survival of few *individuals*, whereas the scientific view emphasises the few *species* that tolerate extreme conditions. This latter feature leads to the recognition that extreme environments have reduced species richness (see Combes & Morand, this supplement).

Almost inevitably, an extreme environment comes to be defined in terms of its effects on the animals that inhabit it (or by the difficulties experienced by animals unable to inhabit it!) rather than by its intrinsic characters. Constraints imposed by the environment could be depicted by plotting along intersecting axes the environmental variables that determine survival of living organisms (in the manner of the niche concept). This would demonstrate a major part of the abundance and diversity of life accommodated within an irregular central 'multidimensional hyperspace' framed by well-recognized limits of temperature tolerance, oxygen and water availability, and so on. 'Extreme environments' would then be represented on the outer margins of space, as satellites where smaller peaks of abundance are created by certain combinations of conditions. Thus, marine environments characterized by high pressure, low temperature, lack of light, etc., are actually occupied by prolific life (in the deep-sea). The organisms that flourish under these conditions do not represent the tails of a normal distribution of adaptation extending from the central hyperspace; instead, they occupy their own 'normal distributions' and may show little or no overlap with the centre. Thus, these satellites may be more-or-less self-contained respectively within their own adaptive hyperspace. The separation of these central and peripheral hyperspaces emphasizes that it is inappropriate to compare putative 'normal' and 'extreme' environments by the same criteria. Each is constructed of different subsets of intersecting environmental gradients and their characteristic organisms are adapted to these conditions and should not be considered as displaced representatives from a different environment.

The term 'extreme environment' is therefore anthropocentric or, more precisely, represents a view from within the set of environmental parameters that accommodates the 'familiar' diversity of life. However, Bray and co-authors (this supplement) point out that, on the basis of its total volume, the abyssal ocean and its inhabitants could be considered to represent the most typical environment of this planet.

Given this rather artificial, but nonetheless practical, viewpoint, there are two distinct components of life in extreme environments. One group of organisms survives extreme conditions as a temporary measure, often as a dormant stage designed to resist hostile factors until the return of conditions in which its activity can resume. To continue the analogy outlined above, these organisms may make a

short-term excursion from their central hyperspace (perhaps as dispersal propagules), or they become isolated from this central zone by unfavourable (sometimes seasonal) conditions. Their adaptations enable them to tolerate extreme conditions but, in their dormant state, they may not actually exploit this environment. By contrast, other organisms can maintain active life in these conditions which represent their natural zone. Transfer of these to different (supposedly less extreme) conditions may exceed their survival range and they die. The distinction between these types of environmental adaptation is discussed further by Perry (this supplement) within the categories 'resistance adaptation' and 'capacity adaptation'.

This supplement considers 'extreme environments' as part of its remit, but to become distracted by the problems of defining 'extreme' would destroy the inherent fascination of a wide range of parasite adaptations. The scope, therefore, is to consider the wider range of constraints that regulate parasite biology and to gain insight into the mechanisms by which parasites may respond to these factors. In association with this, the supplement aims to highlight less familiar examples, taken from natural host-parasite systems, to provide a glimpse of the wider zoological and evolutionary view of the diverse and often ancient lineages of animal parasites.

Physical environmental conditions

The nature of many parasite life cycles, where a transmission stage is released into the external environment, produces a requirement to survive in the absence of the host and often, therefore, to tolerate adverse conditions. Perry documents how the ability to survive different environmental stresses, including low and high temperatures, lack of oxygen, osmotic stress and dehydration, may be linked by common mechanisms. It follows from this that the animal phyla that are specialists in these mechanisms – including the nematodes, tardigrades and rotifers – can survive a range of the most severe stresses. For this supplement, two examples of extreme physical conditions have been chosen to illustrate these features with respect to parasite adaptation: low temperatures and desiccation. Reviews by Wharton and Perry document adaptations that fascinate both the biologist and the layman, permitting life to be sustained in circumstances where death should be inevitable. Wharton records how freeze-avoiding, supercooled potato cyst nematodes can survive temperatures as low as -38°C ; larvae of a nematode parasite of reindeer survive freezing at -80°C ; larvae of *Trichinella nativa* remain infective in host tissue at -18°C for four years. The mechanisms are varied; some nematodes enter a state of anhydrobiosis, where there is no water to freeze, and this strategy

overlaps with that involved in desiccation survival. Perry notes that where water content falls below about 20% there is no free water in cells. The 20% of bound water is involved in the structural integrity of macromolecules and macromolecular structures such as membranes. It is remarkable, therefore, that the water content of desiccated, anhydrobiotic nematodes may be only 1–5%, indicating that the bound water has been lost. Some plant parasitic nematodes, such as *Ditylenchus dipsaci*, demonstrate the most spectacular abilities for long-term survival, remaining viable after 23 years storage in dry plant material. These are the mechanisms that would aid the transport of living organisms through space!

Macro-environmental conditions

Temperature has an all-pervading influence on parasite life cycles, regulating rate-dependent processes of stages in the external environment and within ectothermic hosts. Only those internal parasites that exploit two classes of vertebrate animals – birds and mammals – are free of this constraint, during the period within their endothermic hosts. Even for these, temperature fluctuations affecting only part of the life cycle are sufficient to exert a powerful control on parasite population dynamics. Some parasite life cycles are adapted to this seasonal inhibition with a strategy that synchronises transmission with favourable environmental conditions and increased host availability. Thus, eggs of the sheep nematode *Nematodirus battus* enter diapause in autumn and overwinter on pasture; hatching of infective larvae requires chilling followed by increased temperatures in spring, and this synchrony enables *en masse* infection of lambs (see Wharton, this supplement). It is not unexpected that low temperatures, especially those approaching freezing point, should represent a major constraint on transmission. However, it is surprising that temperature-induced inhibition of parasite transmission may begin at temperatures as high as 10 °C. This is illustrated by representatives of three diverse groups of helminths: monogeneans, digeneans and nematodes. In species of *Discocotyle*, *Fasciola* and *Ascaris*, development of stages exposed to the external environment is extremely slow or ceases below 10 °C (indeed, in *Ascaris suum* this threshold is 15 °C) (Gannicott & Tinsley, 1998*a, b*; Ollerenshaw, 1974; Larsen & Roepstorff, 1999, respectively). In each case this affects the eggs, and hence the generation of infective stages, but also the intra-molluscan stages of the liver fluke. For *Discocotyle*, development and maturation of worms established on the fish host is also interrupted and output of eggs by previously-matured parasites is minimal. Transmission of *Ascaris* and *Fasciola* to the final hosts may continue from the pool of infective eggs and still-viable cysts that completed develop-

ment before the decline in temperatures, but the rate will be greatly reduced. The remarkable outcome is that, in equable temperate climates as in Northern Europe, host-to-host transmission is almost eliminated for half of each year, from early November until late May. Since each of these parasites is responsible for significant disease under appropriate circumstances, the corollary is that transmission during the other half of each year is very successful in generating high worm burdens. The case study outlined by Tinsley, based in the Sonoran Desert of North America, illustrates the same effect: here, the threshold temperature for parasite development and reproduction is 15 °C and, in exact parallel, all life cycle progress is precluded between October and April each year. The extent of this inhibition is counterintuitive. An evolutionary biologist might predict the strong selective advantage of life cycle adaptations that would enable exploitation of a greater proportion of each annual cycle.

Given this documentation of temperature-dependent regulation of transmission, it is fascinating to encounter data demonstrating continued transmission under exceptionally severe conditions. In the high Arctic, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) experience a long cold winter: typically the upper metre of ground is frozen and snow-covered from October to the end of May or early June. Transmission of trichostrongyle nematodes would be expected to be low. However, Halvorsen *et al.* (1999) recorded an increase in total abundance of infection over the winter, indicating that reindeer continue to ingest infective larvae from snow-covered pasture. They considered it unlikely that there is significant larval development below freezing point, but the infective stages have a relatively high survival rate at these temperatures so transmission probably involves larvae that developed to the infective stage during the preceding summer and autumn. One implication of the overwinter transmission in Svalbard is that progressively increasing worm burdens may induce disease in late winter when reindeer are also stressed by limited food availability and when their immune response may be reduced. This contrasts with the outcome well-documented for related parasites in domestic livestock where temperature constraints inhibit overwinter transmission: in these cases, hosts have respite from accumulation of infection at a time when environmental conditions may prejudice the ability to cope with disease. In ectothermic vertebrates, the temperature dependency of the immune response adds another component to the host-parasite interactions that are regulated by seasonal temperature cycles. This is explored in the paper by Tinsley. In the monogenean *Pseudodiplorchis americanus*, pathogenic effects (caused by blood-feeding) are parasite size dependent; growth inhibition during the period of low temperatures

therefore prevents any increase in disease effects. Parasite blood consumption is also temperature-dependent, so that energetic demands on the host are minimal during winter. However, coincidentally, temperature-induced suppression of the immune response allows worm burdens to survive, whereas an equivalent period at higher temperatures would lead to elimination of the entire infection. A special concern of this supplement is to document information such as this, indicating the complexity of host–parasite interactions in the natural environment.

Studies based in a hot desert (in Arizona) would be expected to demonstrate major environmental constraints on parasite biology, especially in a case where transmission occurs in water. The paper by Tinsley begins by documenting remarkable specializations associated with achieving synchrony of life cycle events with briefly favourable environmental conditions. Fortuitously, during a long-term study of the host and parasite populations, it became possible to follow the effects of a period of exceptional drought. The impact was evident in a succession of years of failed recruitment, leading to local extinction of previously-stable parasite populations. It might be concluded that this provides the most dramatic illustration of the power of extreme environmental conditions, leading to extinction despite finely-tuned adaptations. However, this paper also reviews the quantitative data now available for this host parasite interaction: aside from the effects of rare environmental perturbation, the major part of parasite pre-reproductive mortality occurs within the host, attributable to immune attack. This suggests the conclusion that the most severe environmental constraint, even in a desert, may actually be a feature of parasite life cycles generally – the conditions created by the host.

Host environmental factors

Alongside inclusion of constraints that are, to any biologist, immediately recognisable as extreme, this supplement aims to highlight other less obvious subjects where specific environmental conditions create very considerable difficulties for exploitation by parasites. Although at first sight the external surface of a fish presents an apparently rather unspectacular environment, its characteristics actually illustrate a series of major constraints affecting ectoparasites. Fish skin is wet, notoriously slippery, and swept by powerful water currents. The task is accentuated for those parasites that must also retain the ability to move – to find a sexual partner or new areas for feeding – as well as maintain secure attachment on the slime-covered surface of a fast-moving fish. Kern presents a comprehensive review of the environment and the survival mechanisms of monogeneans that inhabit fish skin. This platy-

helminth group has become specialized in the deployment of hard, proteinaceous hooks borne on a posterior disk-like haptor to pin themselves to the host. Kern correlates the form and function of these hooks to the microscopic structure of the host's skin. Tiny marginal hooklets have blades that pierce the apical membrane of host epithelial cells and become embedded in the terminal web of tonofilaments just below the cell surface. The terminal web is sufficiently strong to resist tearing of the cell. The load is spread by employing multiple points of attachment to the epidermis, typically 14 or 16 hooklets, and this arrangement is very successful – as judged by its highly uniform organisation amongst monogeneans – for the attachment of small skin parasites (generally not exceeding 300 μm in body length). With increasing size, many monogeneans rely on a second series of hooks, the much larger hamuli, that may penetrate through the host epidermis and its collagenous basement membrane into the fibrous dermis beneath. Monogeneans employ two further mechanisms for attachment, often complementary to sclerite penetration: muscular suction and sticky secretions. The latter represent a particularly fascinating aspect of the biology of monogeneans. Kern describes how, apparently against all odds, monogeneans employ adhesive secretions to attach to the mucus-covered and water-current-swept skin surface. In *Entobdella soleae*, two distinct secretions are discharged at the attachment site and their mixing generates adhesion reminiscent of that effected by the interactive components of commercial epoxy resins. The cement layer is 4 or 5 μm thick and penetrates between the microridges of the host's epidermal cells and between the microvilli of the parasite's adhesive pads. The bond is sufficiently strong to resist powerful water currents and yet, even more remarkably, the parasite is able to sever the adhesion instantly during its leech-like locomotion. Dissolution of the cement is mediated via the apical membrane of the adhesive pad tegument and a third secretion could provide the means of release.

These are problems encountered by marine engineers who require adhesives that will operate instantly underwater, but the parasites have taken this technology one stage further in producing a mechanism that can instantly dissolve the bond. The adaptations provide an exciting example of the way in which fundamental research may have important commercial applications.

Kern's review also illustrates the reciprocal nature of host–parasite interactions. Fish skin appears highly vulnerable to parasite infection; however, those features that appear to increase its vulnerability – exposed living cells and proximity of blood vessels – may also be associated with powerful immune responses. Recent immunological studies suggest that the skin of fishes has a secretory defence system independent of the systemic system. This is

likely to be a major factor influencing host specificity, site specificity and the regulation of infection levels. This theme, the environmental constraint created by host immunity, leads to consideration of the lethal conditions generated by the host immune response. Combes and Morand develop the idea that parasites themselves have created these hostile conditions within hosts by having driven the evolution of the immune system. They argue that parasites have responded to 'genes to kill' by 'genes to survive', and this has triggered selection of measures and countermeasures that form the basis of a continuing coevolutionary arms race.

Understanding of the interactions between the killing mechanisms of the host and the survival and manipulative strategies of the parasite contributes to a relatively well-reviewed area of parasitology, including the recent *Parasitology* supplement (Doenhoff & Chappell, 1997). This supplement does not intend to duplicate any of this well-established information. Instead, a paper by Riley focuses on an 'unconventional' case study involving an ancient parasite group, the phylum Pentastomida, whose adults infect the respiratory tract of tetrapod vertebrates, principally reptiles. Although the delicate pulmonary epithelium and rich blood supply might appear to provide a favourable environment for macroparasites, Riley points out that relatively few helminths have colonized vertebrate lungs to reside in or on the respiratory epithelium (aside from those, principally larval nematodes, that penetrate the lungs in transit to the gut). A range of protective mechanisms are involved in lung homeostasis. A key component is pulmonary surfactant, a complex mixture of phospholipids, neutral lipids and proteins. This has an essential biophysical role and is also crucially involved in protection of the lungs from infection. Lung-dwelling pentastomids are typically large (some are 5–10 cm in length), long-lived (in some cases many years), and feed on blood from the pulmonary capillaries. Surprisingly, they cause little observable pathology. Riley documents evidence suggesting that these parasites evade immune surveillance and reduce inflammation by secreting their own surfactant. This has a lipid composition very similar to that of lung surfactant and coats the parasite's cuticle with material that is therefore immunologically compatible with host secretions.

Most of the recent developments in parasite immune evasion and exploitation are based, for reasons of major medical importance and research funding, on a relatively small number of intensively studied human parasitic diseases, and most of these are studied, for reasons of practical expediency, in laboratory rodents. Riley's account provides a glimpse of interactions in the rest of the parasitological world; it should contribute to the prediction that there must be an enormous diversity of parasite adaptations to counter what is, arguably, the domi-

nant environmental influence on parasites: the host immune response.

Evolutionary considerations

Several of the reviews emphasise evolutionary aspects of host-parasite interactions. Combes and Morand link the concept of the hostile niche with the specialization of parasites to survive in a limited number of these environments and, hence, the characteristic of host specificity. Kearns follows this idea in relation to the influence of the defensive responses of fish skin on the host ranges of monogeneans. The case studies employed in some papers also highlight the very long evolutionary association of particular host and parasite groups. For monogeneans, the association with their fish hosts may extend back to Palaeozoic times, before the modern lineages of fish had emerged. Pentastomids have the distinction, very rare amongst parasite groups, of a fossil record: this provides a tantalizing glimpse of forms present in the Cambrian. This evidence points to an enormously long period of natural selection and specialization.

It is logical, therefore, that further consideration of parasite responses to environmental constraints should take a phylogenetic perspective. Jackson pursues the concept of host specificity as a reflection of the constraints that restrict parasite occurrence in nature; he notes the potential for host specificity to change over evolutionary time, with new host lineages acquired and others lost. Changes of host by parasites are events of intrinsic evolutionary interest and may have had an important influence on present parasite distributions. Jackson critically evaluates the inference of host-switching from phylogenetic data.

The deep-sea environment presents exceptional constraints on life (at least, life as it is known nearer to the surface), including physical conditions such as high pressure, low temperature and lack of light. For parasites there are the additional factors of a sparse distribution of potential hosts, highly specialized food chains, and the characteristic that there is no 'platform' on which transmission can occur. Because of this lack of a surface on which parasite eggs may settle and develop and from which new hosts may be invaded, all life processes must take place 'on the run'. Bray and co-authors document the records of digeneans in the teleost fishes that inhabit the deep-sea and note the distinctiveness of this parasite fauna. They employ molecular phylogenies as a means of making inferences about the origins, routes and frequency of invasion of the deep-sea. They also review some of the adaptations for survival, including the nature of life cycles. This concluding paper fulfils one of the aims of this selection of studies, in providing a new, thought-provoking,

insight into consideration of parasite adaptation. In case one might lightly dismiss the deep-sea fauna of hosts and parasites, Bray and co-authors emphasize that over half of the earth's surface is covered by the deep-sea with a depth of over 3200 m. There is enormous faunal diversity, including potential intermediate hosts such as molluscs, annelids and arthropods. The impression is clearly conveyed, as in some other areas of parasitology, of how little is still actually known.

Where harsh conditions are 'unrelenting', it might be predicted that animals regularly inhabiting such environments have appropriate adaptations to counter the constraints: the proof of their specializations must be assumed from their continuing survival. It might be argued that, by contrast, conditions that are really 'hostile' are those that occur sporadically, where life-threatening circumstances are unexpected (for instance, in temperate areas, a sudden period of freezing in late spring). Sometimes, the final challenge may follow the stress of already-difficult conditions: effects are exacerbated by existing weakness. A series of phrases in the English language express this concept, including 'the last straw breaking the camel's back'. In the scenario recorded by Tinsley (this supplement), conditions of sufficient severity to cause local parasite extinction could be attributed to a succession of unfavourable circumstances, the worst in a 35-year record of weather conditions ('a run of bad luck'). These are the conditions that test adaptations 'to the limit', and these events provide the basis for natural selection of genotypes most fit to cope with a recurrence of these circumstances.

Apart from its intrinsic interest, understanding the environmental constraints that limit parasite populations has wider importance. Removal of some of these constraints, especially those that limit transmission efficiency, has been a major contributory factor in the imbalance involved in parasite-induced disease in the medical and veterinary arenas.

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