Chapter 2
Defining the Concept of a Species Physiological Boundaries and Barriers

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Abstract This chapter presents the concept that physiological boundaries can be described for each species based upon the evolutionarily established capabilities and metabolic needs of that species. This concept is envisioned as a vital boundary consisting of a center point enveloped by two concentric theoretical closed surfaces. The boundary center represents optimum environmental conditions for that species, enabling members of the species to achieve their normal longevity. Suitability of the environmental conditions lessens with outward distance from the boundary center. The species inner vital boundary surface defines the minimum limit of environmental conditions which would allow a sufficient longevity for achieving numerical replacement. Physical locations where the environmental conditions meet the requirements either for inclusion within the inner boundary region which is encompassed by the inner vital boundary, or equate the inner vital boundary itself, would represent potential habitat areas for that species. The outer vital boundary represents combinations of environmental conditions which allow members of the species a survival time of 1 min. Physical locations meeting the environmental requirements for the interboundary region, which lies between the inner and outer vital boundary surfaces, represent areas where that species could survive only temporarily. Physical locations where the environmental conditions are beyond the outer vital boundary represent barriers to movement by that species. Two species could interact in nature only if their vital boundaries overlap. These boundaries theoretically could be depicted mathematically. Calculations estimating conditions just inside the outer vital boundary would have application for ascertaining short term survival under extreme conditions.

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2.1 Introduction

Species differ with regard to the habitat locations in which they live, and in large part such ecological differences result from the ways in which those species have evolutionarily adapted to survive in accessible environmental locations (Grinnell 1917, Hutchinson 1957). This chapter offers one perspective for studying those differences by presenting the concept that each species can be described as having physiological boundaries defined by the evolutionarily established physiological capabilities and metabolic needs of that species. This concept is envisioned as a vital boundary consisting of two concentric theoretical closed surfaces. For the purpose of illustration I have represented this concept in Fig. 2.1 with those surfaces depicted as two concentric polyhedrons. The surface of the inner polyhedron represents the species inner vital boundary. The surface of the outer polyhedron represents the species outer vital boundary. There would be a centerpoint for the inner polyhedron, which would represent the center of the species boundary, but for lack of artistic skill I have not depicted that centerpoint in Fig. 2.1. The favorability of environmental conditions is presumed to be optimum for a given species at the center point of their inner vital boundary.

Biologists and environmental microbiologists often become accustomed to thinking of a species habitat in terms of geospatial coordinates, and thus we mentally pin species to a permanent map location just as museum specimens get pinned into a fixed location within an exhibiton case. When we pin species to a map location we do not account for the fact that environmental conditions at the identified location will change over the course of time, and species must be allowed to move when those conditions change. Otherwise, our geospatially pinned species would reach the same fate as do museum specimens, existing only as evidence of what once had life. One of my goals in presenting this habitat definition concept is removing those geospatial pins by offering an alternative, which is to understand the criterion that define a species choice of where it resides.

According to this habitat definition concept, members of a species would have a predictable average population longevity time (L_t) for each combination of environmental conditions to which they were exposed. At the center of the species vital boundary the favorability of environmental conditions would be optimum, and correspondingly the expected longevity time for members of the species would be greatest. When living under the conditions at the center of a species boundary, members of that species potentially could achieve their average normal longevity (L_n). The favorability of environmental conditions decreases as the mathematically defined distance increases from the center of the boundary outward. The surface of the inner polyhedron shown in Fig. 2.1 represents the species inner vital boundary, where the environmental conditions are minimally adequate for members of that species to experience the average longevity they would require from birth in order to achieve numerical replacement (L_r). Although the maximum radius from the centerpoint outward theoretically would be infinite, in a practical sense we would need to presume that population survival time has some functional lower limit. The

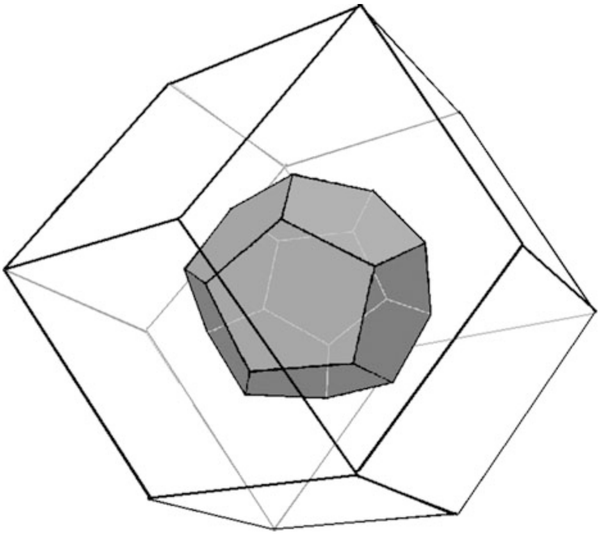

Fig. 2.1 Inner boundary depicted within an outer boundary. This illustration depicts the concept of a species having an inner vital boundary concentrically located within an outer vital boundary. The boundaries would be theoretical closed mathematical surfaces with the axes of these polyhedrons potentially representing some of the environmental variables that would be used in defining those boundary surfaces. The boundary surfaces would be less symmetrical than depicted here. Also, the mathematical distance between the inner and outer vital boundary surfaces would not be uniform

outer polyhedron outlined in Fig. 2.1 would represent the surface of the species outer vital boundary, where the evironmental conditions are adequate for members of that species to experience an average longevity of one minute and that survival duration has been chosen as the functional lower limit for longevity. Thus, L_t equals L_n at the center of a species boundary, L_t equals L_r at the surface of the species inner vital boundary, and L_t equals 1 min at the surface of the species outer vital boundary. By presenting each L_t value as an average, I allow each of those values to have a statistical deviation range which can account for variation between individual members of a species and also can account for differences between subpopulations of a single species.

The members of a species are obliged to live within their species vital boundaries. This concept of boundaries is not something marked out as if a territory on a map, it is instead a statement of the functional requirements and limitations of that species. From the perspective of a given species, any geographically or otherwise identifiable physical locations which satisfy either requirements of the inner boundary region which is encompassed by the surface of the inner vital boundary, or at minimum the environmental conditions of the inner vital boundary itself, would represent areas where members of the species potentially could have a permanent residence. Those physical locations would be potential habitat areas for the species because the environmental conditions in those locations could allow members of the species to have sufficient longevity for completing their normal replicative cycle. Many species have evolutionarily established inner vital boundary conditions that allow a very broad range of suitable habitat locations. Contrastingly, in the case of some symbiotic microorganisms, the species inner vital boundary conditions may limit the members of that symbiont species to permanent residence only within a few specific tissues of certain host species. A species continually must find at least one habitat location in which its members successfully can reside within the requirements of their inner vital boundary, because otherwise that species would become extinct.

From the perspective of a species, any physical locations which satisfy either the interboundary region which spans between the inner and outer vital boundaries, or at minimum the environmental requirements defined by their outer vital boundary, would represent places where members of the species could survive but only temporarily rather than permanently. Those places have only temporary suitability for the indicated species because a population of that species could not survive to complete its life cycle under such relatively inadequate conditions and thus the species population eventually would be fated to die off unless the members of that species could transition to a more suitable location.

Physical locations where the environmental conditions are beyond the outer vital boundary of a species represent barriers to movement by that species. While a particular species cannot survive in a metabolically active condition for very long beyond its own outer vital boundary, its habitat locations may be sufficiently diverse that while moving within their habitat the members of this species may cross the boundaries of many other species. This overlap of boundaries allows biological interactions between the members of different species.

From the perspective of this habitat definition concept, the mathematically representable boundaries of a species will have been established by evolution and those boundaries remain fixed. The physical locations which are adequate for habitation by a species will, however, shift with changing environmental conditions. Species do tend to evolve survival mechanisms that allow their members to successfully shift their physical location as changing environmental conditions shift the physical locations of their pertinent barriers so that a species will not become trapped beyond its outer vital boundary. The only way for members of a species to survive the conditions beyond their outer vital boundary is by having developed a metabolically inert survival structure. Examples of such structures are bacterial endospores and viral capsids. The vital boundaries of a species can be moved only by that species undergoing further evolution. Many species indeed have moved their boundaries through evolution and thereby successfully crossed existing barriers.

2.2 Further Understanding the Nature and Limitations Imposed by Boundaries and Barriers

The fact that a particular physical location meets the environmental conditions required for permanent residence by some given species does not mean that the suitability is unchangeable. Environmental changes can be either permanent or cyclical, and those changes often result in the need for species to develop migrational capabilities. Examples of seasonal migrations are those made by species of bats, birds, caribou, and whales. In the cases of migrations by monarch butterflies and maple trees (Pitelka and Plant Migration Workshop Group 1997), no individual member of the species completes a full migration cycle. The capability of a species' members to migrate also facilitates colonization of new areas. Cyclical migrations could be viewed as highly evolved forms of dispersal. And, as the macroorganisms migrate, so too must there be a corresponding migration of those microbial species whose lives are either dependent upon or interdependent with the migrating macrobes. Successful migration requires an absence of physiologically defined barriers that could block the migrational routes.

Suitable residential locations for a given species may be either contiguous or separated by barriers and what represents a barrier to one species many not represent a barrier to some other species. Figure 2.2 presents one aspect of the concept that barriers often separate those locations which could represent potentially suitable habitat locations for a species. The outer vital boundary for the big cats extends some distance from the shoreline, provided that either the water depth is sufficiently shallow that the animals could walk or the distance is not greater than the cats capacity for swimming. An expanse of water which exceeds the travel limitations of the big cats will represent a barrier for those cats. The shoreline represents a barrier from the perspective of sharks because they have no terrestrial capabilities. For some aquatic reptiles such as sea turtles, and fish such as the grunion (genus *Leuresthes*), their species inner vital boundary spans the shoreline as evidenced by the fact that those aquatic species lay their eggs on the land. The fact that Grunion rely upon aquatic respiration makes them susceptible to quickly suffocating if they strand when spawning on the land surface, a vulnerability which suggests the mathematical distance between their inner and outer vital boundaries may be relatively small with regard to this aspect of their environmental requirements.

2.2.1 Barriers Are Not Fixed in Location and Time

Barriers determined by the physiological capabilities and metabolic requirements of a species often can be physically defined and determinable by physical measurements. An example of the tangible nature of many barriers is the fact that a species' oxygen (molecular oxygen) requirements may turn geographical features such as

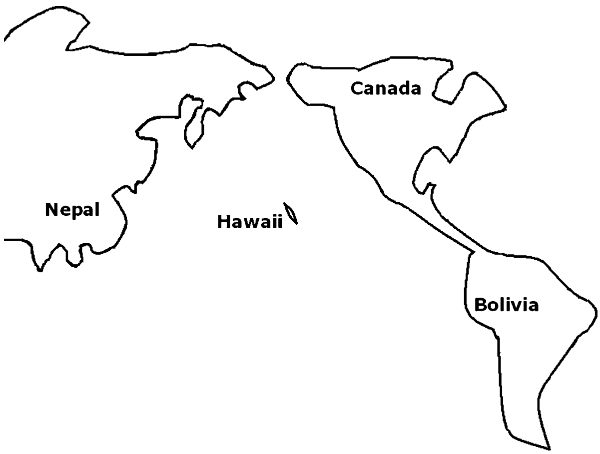

Fig. 2.2 Big cats and sharks. This illustration has been given a humorous title, but represents the concept that for each species there potentially might be many different places that could serve as suitable locations for residence. Unfortunately, it may not be possible for a single species to reach all of those locations. The depiction here is of mountain dwelling cats which could move by land connection between the Canadian Rockies and South American Andes. An insurmountable aquatic barrier currently prevents large cats from moving between the Americas and the Nepalese Himalayas. Mountain dwelling cats have not crossed the aquatic barrier which blocks them from reaching the Hawaiian mountains. Sharks can reach all of the land masses but the shoreline represents a barrier which they cannot cross

either high mountains or shorelines into barriers. It is important to remember that the physical locations of barriers are not permanently fixed. Some barriers may shift and others even disappear as with the rise and fall of mountain ranges and water surface levels. Some types of barriers have a relatively short term cyclical occurrence resulting from either tidal, daily, seasonal, or annual climatic fluctuations. Examples of short term cyclical barriers would include those produced by weather patterns including temperature and changes in precipitation; the presence, levels and flowrates of surface and subsurface water including tidal patterns; thermoclines and haloclines. Other cyclical changes have longer periodicity such as those which involve glaciation cycles and plate tectonic movements.

We humans have shown an exceptional capability for cultural evolution which has allowed us to survive in physical locations that would otherwise be too inhospitable. Controlled combustion (Berna et al. 2012), insulating clothing (Toups et al. 2011), and the use of containers as means for storing water have allowed us to establish permanent residence in geographical locations where we otherwise could reside only temporarily. These same technological achievements plus additional developments including the invention of boats as a mode of transportation, the ability to store and carry breathable atmosphere, climbing equipment, and pressurized suits have helped us to travel beyond our species natural geographical barriers and survive in locations where the ambiental environmental conditions are well beyond our outer vital boundary. It is important to understand that an astronaut in deep space who is wearing a pressure suit hasn't really changed his vital boundaries, he is just ensuring that those vital boundary conditions are satisfied within his suit.

The capacity of our species for accomplishing cultural evolution has expanded our abilities in many regards, enabling us to interact with other species whose vital boundaries do not overlap with our own outer vital boundary. However, if inability to cross a physiologically defined barrier precludes movement of a particular species from an unsatisfactory location to some suitable location, and presence of the barrier does not change, then that species must hope to move its vital boundaries. The presumptions are that a species vital boundaries are fixed by biological evolution and that movement of a species vital boundaries can be achieved only through further biological evolution.

2.2.2 Understanding the Factors that Define a Species Vital Boundaries

The concept of a species vital boundaries includes a complicated mixture of factors and sometimes those factors are very highly species specific. Table 2.1 lists some examples of environmental factors that are useful in understanding the vital boundaries of a species. Such environmental factors visually could be represented by the axes of the polyhedrons depicted in Fig. 2.1 and those factors could be employed as variables for calculating population survival time as described later in this chapter. Thus, Fig. 2.1 helps with understanding the conditions of the boundary center, inner boundary region, inner vital boundary, interboundary region, and outer vital boundary. Figure 2.3 is intended to help with understanding how an overall optimum combination of environmental conditions defines the center of a species vital boundary. When examining Table 2.1 and Fig. 2.3 it is important to consider how individual environmental factors, which can be considered and represented as mathematical variables, affect the survival conditions for an individual species.

It is important to notice that micronutrient minerals are included in Table 2.1 because they would be considered natural environmental factors. Other micronutrients such as vitamin C (World Health Organization 1999), which are organically generated by food species and acquired by ingesting those food species, are of key importance but I have not considered those food-generated micronutrients as being environmental factors for the purpose of this proposed concept. Similarly, neither the availability of food species, nor presence of predators, nor infectious disease are included in the estimation of L_t values because they also are not being considered as environmental variables for the purpose of this proposed concept. Thus, there are limitations when using this proposed concept for stating whether or not the combination of environmental factors which describes a physical location would suggest that location to represent an adequate habitat for allowing some species to achieve either their L_n or L_r. The environmental

Table 2.1 Examples of environmental factors representing variables for use in understanding vital boundaries

Factors with potential applicability to all species
Ambiental temperature
Ambiental external body pressure
Ambiental level of ionizing radiation
Distance to suitable resting surface
Inclination angle of the surface
Potential for adherence to the surface
Potential toxicity of the surface
Heavy metals including those representing micronutrient minerals
Natural and synthetic toxins (includes antibiological compounds)
Photoperiod
Level of specifically required wavelengths for photosynthesis
Factors which could apply to species using terrestrial respiration
Atmospheric gases
Carbon dioxide
Carbon monoxide
Chlorine
Oxygen
Ozone
Sulfur dioxide
Distance to available drinking water
Flow velocity of the surrounding atmosphere
Humidity
Precipitation
Factors which could apply to species using aquatic respiration (includes microbes living in liquid medium)
Dissolved gasses
Carbon dioxide
Carbon monoxide
Oxygen
Ozone
Sulfur dioxide
Dissolved halogens
Chlorine
Iodine
Flow velocity of the surrounding water
pH
Salinity

conditions in that location might be entirely suitable, but the species might not thrive in that location for other reasons including absence of food species, predation, and also competition against other species that have similar niche requirements.

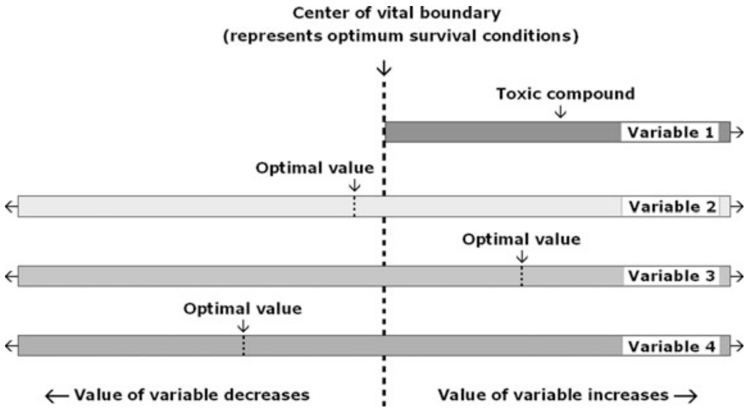

Fig. 2.3 Center of vital boundary relative to optimal parameter values. This figure gives a hypothetical representation of how the parameter values of different environmental variables relate to the expected longevity for members of an example species. Most of the individual environmental variables which are important in defining the boundaries for a given species will have a survivable parameter range and optimal value. Some of the variables could be considered unidirectional, signifying that the deleteriousness of variance from the optimal value is assessed in only one direction as represented by Variable 1. Toxic compounds such as pesticides and antimicrobial compounds would be representative examples of variables that qualify for unidirectional assessment because their optimal parameter value may be zero and any presence of the compound acts to decrease survival of the affected species. Most variables will be assessed bidirectionally, signifying that the deleteriousness of variance from the optimal value would be assessed in two directions. Variables 2 through 4 depicted in this figure would be assessed bidirectionally. Conceptually the center of a species vital boundary represents its optimum environmental conditions and allows members of that species the possibility of surviving to fully realize their normal longevity

2.2.2.1 Defining Those Factors as Mathematical Variables

If we reflect upon the suitability of an available resting surface (yes, pun intended) as one example of the factors listed in the Table 2.1, many aquatic species seemingly need no resting surface. This same example factor can have only a plus or minus influence for numerous other species that we might consider, such as many microbial species which survive best in a biofilm (Huq et al. 1983, Kiørboe et al. 2003, van Schie and Fletcher 1999), and some of the sessile aquatic invertebrates which physically attach to their resting surfaces, of which both groups prefer having the presence of a suitable surface but may seem unaffected by the inclination angle of the surface onto which they have become attached. However, the inclination angle of the resting surface does affect numerous species in a unidirectional sense meaning that the optimal may be zero, any deviation from zero is detrimental, and the deviation effectively can be measured in only one direction. A consideration would be species for which a surface angle of zero inclination may be optimally required and increasing the deviation from that optimal inclination angle will make the surface less suitable although assessing that angular deviation as positive versus negative is unimportant because falling off to one side of a physical surface is equally deleterious as falling off to the other side. As one general example, many aquatic species such as water striders of the family Gerridae reside by resting at the water surface and unsteady water surface angles due to water turbulence may make the surface unsuitable for meeting the requirements of that species.

Interactions between species occur in locations where the environmental requirements of the involved organisms, and thus their vital boundaries, overlap. Species often differ with regard to the variables which define their environmental requirements. Determining the likelihood of boundary overlap and thus potential for interaction between the members of two species requires the use of common variables along with an understanding of the parameter value ranges required by the two species. Even when the parameter value ranges of most environmental variables generally would suggest that a physical location either meets or exceeds the requirements for being encompassed by a species inner vital boundary, a single key factor can make a huge difference between the ability for two species to interact. I once viewed a television program which showed a fox chasing a goat onto a rocky hillside. The goat species represented customary prey for the fox species. But, when the goat climbed onto a steep rock outcropping upon which the fox could not stand, the fox abandoned the pursuit. Clearly, in that one aspect the species otherwise similar vital boundary requirements did not overlap because the surface conditions of the rock outcropping were beyond the outer vital boundary of the fox, and thus the inclination angle of that surface represented a barrier which blocked interaction between the goat and fox. Ionizing radiation (United States Nuclear Regulatory Commission 2015) and also many toxic compounds (Health and Safety Executive 2013) seem to affect species in a unidirectional manner, meaning that the ideal level of exposure to that factor is zero, and there are no measurable parameter value ranges below zero. There are still other environmental factors that may either be essential for a species survival or generally considered benign, but which seemingly can become unidirectionally toxic beyond a given parametric value range particularly as a combination effect. An example of that category would be nitrogen (molecular nitrogen), which to our species is innocuous in a normal concentration at typical atmospheric pressures and we generally seem unaffected by either low atmospheric levels or partial pressures of nitrogen, but nitrogen becomes toxic to us at higher environmental pressures (Edmonds et al. 2013).

Most environmental variables, however, affect species in a bidirectional sense meaning that an optimal value for the variable can be determined and that optimal value is likely to be near the center of the species vital boundary. For a bidirectionally affecting variable, the suitability of environmental conditions for a given species progressively lessens as the parameter value for that variable either increases or decreases beyond the optimal value, eventually reaching either an upper or lower parameter value which only minimally allows the species to have permanent residence (the species inner vital boundary), and potentially reaching either an upper or lower parameter value beyond which the species functionally cannot survive (the species outer vital boundary).

There are species for which surface inclination angle might either be bidirectional or only apparently bidirectional. As an example, some plants prefer to grow in sloping soil for reasons of soil drainage. In those cases, the soil surface inclination angle might only appear to be bidirectional because soil water retention has several definable component variables including porosity (Mohanty and Mousli 2000) that are bidirectionally affective. The contact angle rather than the inclination angle of a surface would represent a bidirectional component that is useful for assessing the possibility of microbes colonizing some types of surfaces, including medical devices (Chandra et al. 2005). Atmospheric oxygen (molecular oxygen) content is another example of an environmental variable which acts bidirectionally. Suggestions for the use of modeling equations to describe how environmental variables affect species survival are presented later in this chapter.

2.2.2.2 Level of Available Atmospheric Molecular Oxygen as an Example Variable

The level of available oxygen, upon which a large percentage of species depend for respiration, can be used as an example variable which has bidirectional effects. Some species use terrestrial respiration, meaning that their oxygen needs must be met by the surrounding atmosphere, while other species use aquatic respiration (Raven and Johnson 2001) which means that they depend upon oxygen dissolved in water. Many microbial species can obtain oxygen from either a surrounding atmosphere or a liquid medium. Macroorganisms tend to be far more physiologically specialized and thus ecologically limited in this regard. There are a few aquatic vertebrate species which normally use terrestrial respiration and successfully also can utilize aquatic respiration (Root 1949). Humans, of course, have evolved to depend upon terrestrial respiration.

Presumably the optimal atmospheric molecular oxygen concentration for our species is 20.9 % at 1 atmosphere of pressure, an oxygen concentration and total pressure which is equal to average sea level atmosphere (molecular oxygen 159 mm Hg; total pressure 760 mm Hg). The safe breathing range for humans is an oxygen concentration of 19.5–23.5 % by volume (Occupational Safety and Health Administration 2015).

Oxygen deficiency results when the level of inhaled oxygen is too low, and oxygen toxicity results when the level of inhaled oxygen is too high. It is difficult to estimate the atmospheric oxygen levels which would represent points on our species inner vital boundary because the lifetime effects of oxygen levels have received little study. But, it is known that humans begin experiencing ill effects at oxygen concentrations of 16 % and below (McManus 2009), which means that an oxygen concentration of 16 % would be beyond our inner vital boundary. For humans, death occurs within minutes at oxygen concentrations of less than 6 % (McManus 2009) which means that an oxygen concentration of 6 % would be just inside our outer vital boundary. Human death occurs within seconds at oxygen concentrations of 4 % and below (McManus 2009), which means that an oxygen concentration of 4 % would be beyond our outer vital boundary. I don't like considering the experiments which would have been performed to produce those results! Humans experience oxygen toxicity effects beginning with oxygen levels of about 53 % (molecular oxygen 400 mm Hg, total pressure 760 mm Hg), with those effects starting as respiratory irritation but progressively increasing in severity at even higher oxygen pressures (McManus 2009), clearly indicating that such high oxygen levels represent environmental conditions that are beyond our inner vital boundary but within our interboundary region.

It is important to understand how the different environmental factors, examples of which are listed in Table 2.1, interrelate. For example, breathing atmospheric air containing oxygen at a partial pressure level which would be normal for us at sea level, will exceed our outer vital boundary at either altitudes where we experience hypobaric conditions (Raven and Johnson 2001) or aquatic depths where we experience hyperbaric conditions (Edmonds et al. 2013) that by definition are too extreme for our species. Physical locations having either those extreme altitudes or depths therefore represent physiologically definable barriers for our species in part because of the way in which our bodies respond to oxygen exposure. The oxygen partial pressure which represents an optimal level for humans at a total pressure equal to normal atmospheric sea level, does instead prove beyond our inner vital boundary at the elevated pressure levels that are used for emergency medical treatments (Patel et al. 2003). The physiological limitations due to pressure related toxicities of molecular oxygen and molecular nitrogen which severely affect the ability of humans to freely venture deep beneath the ocean surface have far less effect upon aquatic mammal species such as Cuvier's beaked whale (*Ziphius cavirostris*) whose vital boundary limits are quite different from ours in many respects. That whale species can dive to 2992 m depth and hold its breath for 137.5 min (Schorr et al. 2014), evolutionarily acquired capabilities which many humans including myself would envy. The critical issue for oxygen dependent species is the oxygen pressure within body organs and tissues (Saglio et al. 1984). Interestingly, we have learned medical usage for the knowledge that tissue oxygen demand decreases with hypothermic conditions (Luscombe and Andrzejowski 2006), representing another way in which different environmental factors interact.

2.2.3 Organisms Which Utilize Other Species as Biological Vectors

The concept of boundaries and barriers as presented here applies to the external environmental conditions which are being faced by the members of a species. As a practical example, anaerobic microorganisms can exist within and interact with aerobic hosts if the internal environment of the host contains zones that are suitably anaerobic. Crossing a physiological barrier to reach a more suitable location, as defined by this theorectical concept, means that a species must survive some

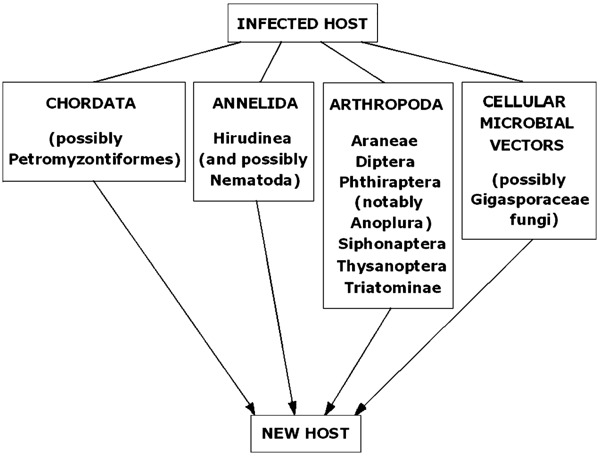

Fig. 2.4 Vectors of infectious disease. Many of the microbial species which are dependent upon biological hosts survive very poorly in the open environment, and thus the open environment represents a barrier which blocks interhost transfer of those dependent species. The evolutionary solution often has been for the dependent species to utilize still other species as vectors for facilitating transmission between hosts. Virus often use their hosts as biological vectors, an interaction that particularly is evident for those virus groups that are capable of residing genomically in near quiescence, as either proviruses or prophage, within a host cell

transition across its outer vital boundary. Figure 2.4 represents the way in which this concept of successfully crossing environmental barriers applies to some microbial species that are dependent upon close physical interactions with biological host species. Of course, not all microbes are welcome guests! Infectious disease is a type of interaction in which a microorganism acts as a parasitic predator and in such interactions the microorganism is referred to as being a pathogen. Both host accessibility and potential disease hazards can change when members of either the potential host species, a potential pathogen species, or a potential vector species crosses a barrier of some other species.

2.2.4 Understanding the Use of Vital Boundaries When Treating Infectious Disease

We intentionally use a variety of approaches that are termed barrier concepts to create obstacles which can lessen the probability of acquisition and transmission of infectious diseases (Hurst 1996, Hurst 2007, Hurst and Murphy 1996). Those types of barriers are classified by their nature as either chemical, physical, or biological, with examples listed in Table 2.2 as described by Hurst (2011). The categories of chemical barriers that are listed in Table 2.2 represent utilization of environmental conditions which exceed the survival limits of the infectious agents. Those

Table 2.2 Barriers to species movement as generally considered from the perspective of preventing infectious diseases

Categories of Chemical Barriers
Ionic (includes pH and salinity)
Surfactant
Oxidant
Alkylant
Desiccant
Denaturant
Categories of Physical Barriers
Thermal
Acoustic (usually ultrasonic)
Pressure
Barometric
Hydrostatic
Osmotic
Radiation
Electronic
Neutronic
Photonic
Protonic
Impaction (includes gravitational)
Adhesion (adsorption)
Electrostatic
van der Waals
Filtration (size exclusion)
Geographic features
Atmospheric factors (includes such meterological aspects as humidity, precipitation, and prevailing winds)
Categories of Biological Barriers
Immunological (includes specific as well as nonspecific)
Naturally induced (intrinsic response)
Naturally transferred (lacteal, transovarian, transplacental, etc.)
Artificially induced (includes cytokine injection and vaccination)
Artificially transferred (includes injection with antiserum and tissue transfers such as transfusion and grafting)
Biomolecular resistance (not immune-related)
Lack of receptor molecules
Molecular attack mechanisms (includes nucleotide-based restrictions)
Antibiotic compounds (metabolic inhibitors, either intrinsic or artificially supplied)
Competitive (other species in ecological competition with either the microbe, its vectors, or its hosts)

chemical barriers thus also represent barriers as defined in this proposed concept by creating environmental conditions that are beyond the pathogens outer vital boundaries. Many of the physical barriers listed in Table 2.2 similarly represent the use of environmental conditions which are beyond the pathogens outer vital boundaries and thus match with this proposed concept of defining barriers on the basis of a species physiological capabilities and metabolic requirements. The use of size exclusion barriers such as filtration, as listed in Table 2.2, represents physical obstacles which are not related to the pathogens vital boundaries even though size exclusion often effectively prevents the movement of species between suitable habitat locations. The biological barriers listed in Table 2.2 likewise are not related to the pathogens vital boundaries and thus not related to this proposed concept of boundaries and barriers.

The goal in treating infectious diseases is to help terminate the infection by decreasing the favorability of the host environment in which the invading microbe is surviving. We often attempt to accomplish that goal by successfully changing the local environmental conditions found either on the surface or within the body of the host. Because such treatments as the use of hyperbaric oxygen, wound disinfectants, and the selective toxins termed antibiotic compounds, represent attempts to achieve local environmental conditions representing either the pathogens interboundary region, or even better the achievement of conditions beyond the pathogens outer vital boundary, then those treatments are encompassed by this proposed concept of boundaries and barriers.

2.2.5 How This Concept of Vital Boundaries Applies to Virus

From the perspective of virus, a host cell can be described as either permissive, semipermissive, or nonpermissive, for a particular virus strain depending upon the extent to which that virus can replicate within the indicated host cell (McClintock et al. 1986). The internal environment of a host cell that is permissive, which signifies the virus can fully replicate and produce progeny virus particles within that cell, would represent the virus' inner boundary region and also the surface of the virus' inner vital boundary. A semi-permissive cell, one in which the virus can replicate partially but not produce progeny virus particles, would represent the interboundary conditions for that virus species. From the perspective of the virus, the cell wall or cytoplasmic membrane of a host cell would represent the outer vital boundary for a viral species because a virus cannot sustain its metabolic activity beyond the intracellular environment. A nonpermissive cell, one in which not even partial replication of a particular viral species is possible, also would have to be considered as representing a location beyond the outer vital boundary of that virus.

2.3 Example Species

The average longevity that can be expected for a particular species under a specified combination of environmental conditions is defined as the species L_t value for that combination of conditions. L_n is the average natural longevity for members of that species under the optimum conditions presumed to exist at the center of its species vital boundary. The goal of this section is comparing the L_t values for each species relative to that species estimate of L_n. If L_t at birth under some combination of environmental conditions equals L_r, which is the longevity required to achieve numerical replacement, then that combination of conditions qualifies as a point on the species inner vital boundary. Any combination of environmental conditions for which a species L_t is one minute qualifies as a point on the species outer vital boundary. Relative survival time is presented here as logarithmically transformed longevity ratio values, given as $\log_{10}L_t/L_n$, and those ratio values describe the expected longevity value L_t for a particular species under a given combination of environmental conditions relative to the normally expected longevity, L_n, for that species. This approach is analogous but not identical to the use of logarithmically transformed survival ratio values in which $\log_{10}N_t/N_o$ (N_o represents the number of individuals alive at time 0 which is the outset of an observation period, N_t represents the number of individuals remaining alive at elapsed time t) is used for describing exponential population decay rates (Hurst et al. 1980) as briefly explained later in this chapter.

I have chosen to give information representing five species as examples, and my selection was of species that similarly are vertebrates and which have at least some degree of overlap in their inner vital boundaries. The example species human, dog, and house mouse, have such strongly overlapping inner vital boundaries that these three species have developed successful commensal relationships and can complete their life cycles within the same room of a dwelling. The Atlantic ridley turtle and red-tail hawk have been chosen to expand the presentation beyond terrestrial mammals. Table 2.3 summarizes the longevity values for these five example species, expressed as $\log_{10}L_t/L_n$, determined for different mathematical distance points from the center of each species vital boundary outward to its outer vital boundary. The following section explains how the values in Table 2.3 were derived.

2.3.1 *Human (*Homo sapiens*)*

The value that I have chosen to use for average global human life expectancy at birth is 67.1 years (United Nations 2013), and that represents my choice of an L_n (average normal longevity) value for humans. The United Nations report (United Nations 2013) indicated that a fertility level of 2.1 children per woman represented our species replacement level. The median of national averages for age at first birth as reported by the Central Intelligence Agency (Central Intelligence Agency 2015)

Table 2.3 Longevity values expressed as $\log_{10}L_t/L_n$ for different mathematical distance points from the center of a species vital boundary outward to its outer vital boundary

Relative outward distance	Example species: Human	Atlantic ridley	Dog	Red-tailed hawk	House mouse
Center of boundary, estimated survival time equals normal species longevity ($L_t = L_n$)	0.0	0.0	0.0	0.0	0.0
Inner vital boundary, estimated survival time equals that required to achieve numerical replacement ($L_t = L_r$)	-3.6×10^{-1}	-5.5×10^{-1}	-6.9×10^{-1}	-5.8×10^{-1}	-9.2×10^{-1}
Survival time ($L_t = 1$ year)	−1.8	−1.6	−1.1	-9.3×10^{-1}	-3.0×10^{-1}
Survival time ($L_t = 1$ month)	−2.9	−2.7	−2.2	−2.0	−1.4
Survival time ($L_t = 1$ day)	−4.4	−4.2	−3.7	−3.5	−2.9
Survival time ($L_t = 1$ h)	−5.8	−5.5	−5.1	−4.9	−4.2
Outer vital boundary, species survival essentially impossible beyond this point ($L_t = 1$ min)	−7.5	−7.3	−6.8	−6.7	−6.0

L_t represents the expected longevity time, which presumably can be estimated for members of a given species under any definable combination of environmental conditions. L_n represents the estimated normal longevity under optimum conditions, which identifies the center of the species boundary. The L_n values used in this representation are: human, 67.1 years; Atlantic ridley, 40.0 years; dog, 12.67 years; red-tailed hawk, 8.5 years; and house mouse, 2.0 years. L_r represents the estimated longevity time required at birth for the members of a species to achieve numerical replacement. The L_r values used in this representation are: human, 29.0 years; Atlantic ridley, 11.15 years; dog, 2.6 years; red-tailed hawk, 2.25 years; and house mouse, 0.24 years

is 22.9 years. Human births are singlets in most instances and thus an average of 1.1 additional births per woman would be required to achieve numerical replacement. I have estimated an average of 3.0 years between human births by the same woman. Tsutaya and Yoneda (2013) have estimated that 2.8 years is required for human weaning, and I presume all offspring would be capable of feeding independently at that time point following birth of the last child. By combining these values relative to human births I have estimated that the longevity humans typically would require from birth in order to achieve numerical replacement (L_r) is 29.0 years, and that has been derived as follows: 22.9 years as median age at first birth, plus 3.3 [equals

3.0×1.1 additional births per woman to reach a replacement number of 2.1], plus 2.8 years for weaning. The human value for L_r/L_n is 0.432 and the value of $[1-(L_r/L_n)]$ for this species is 0.568, which means that on average 57 % of the normal human lifetime remains at replacement age.

The human life expectancy values used in this chapter are from the United Nations report (United Nations 2013), and they represent the average life expectancy at birth for the period of 2000–2005. It is important to avoid making broad mathematical assumptions based upon statistical values that pertain to only subpopulations of a species, and for that reason I have tried to use estimates of both species longevity and also numerical replacement age that are as broadly representative as might be possible. The global estimate for average human life expectancy at birth is 67.1 years and that number has been used in this study as the normal longevity, L_n, value for humans. The greatest national life expectancy listed in that report was for Japan, which had an estimate of 81.8 years. The least national life expectancy was for Sierra Leone, which had an estimate of 40.1 years. My choice of using the estimated global human life expectancy at birth, which is 67.1 years, as the general estimate for human L_t at birth under optimum conditions means that 67.1 years is the L_n for humans. Resultingly, by definition the estimated relative survival time for humans expressed as $\log_{10}L_t/L_n$ is zero when 67.1 years is inserted as the L_t value. If instead I were to use the L_t values at birth for individual countries and the global L_n value, then the $\log_{10}L_t/L_n$ value at birth would be 0.086 for those humans born in Japan, where longevity is estimated at 81.8 years. The corresponding $\log_{10}L_t/L_n$ value at birth would be -0.223 for those humans born in Sierra Leone, where the longevity is estimated at 40.1 years. Our conclusion from those individual nation longevity values might be that environmental conditions are more favorable for humans born in Japan, but in fact other variables such as nutrition and availability of health care may be more important in understanding the human longevity differences between these two countries. In either case, for both Japan and Sierra Leone the human L_t at birth is greater than the L_r for humans, indicating that environmental conditions in both countries should be suitable for permanent residence by humans. That presumption of suitability could be distorted if we considered only the human fertility estimates for individual nations rather than their national L_t at birth. The United Nations report (United Nations 2013) indicates that world wide human fertility (average number of children per woman) for the 2005–2010 time period was 2.53. The fertility numbers for individual nations were 1.34 for Japan and 5.16 for Sierra Leone. Using only those fertility numbers for individual countries rather than the national L_t values as an assessment of environmental suitability incorrectly would produce a conclusion that the environmental conditions in Japan are inadequate as habitat for humans, because humans do not achieve numerical replacement in Japan. That same incorrect conclusion also could result if age at first birth rather than L_t was used as the indication of environmental suitability. Information for human age at first birth from a Central Intelligence Agency report (2015) indicated that the 2012 estimated age at first birth in Japan was 30.3 years while the 2013 estimated age at first birth in Sierra Leone was 19.2 years, and we incorrectly might think that environmental conditions in Japan correspondingly are less conducive for human fertility. Social pressure rather than environmental suitability factors is more likely to be the controlling reason for these differences in age a first birth between Japan versus Sierra Leone.

2.3.2 *Atlantic Ridley (***Lepidochelys kempii***)*

The value which I have used as the estimated average normal longevity, L_n, for this marine turtle species is 40 years and that is the mean of the 30–50 year range estimate (Texas Parks and Wildlife Department 2015). The estimates for age at maturity for this species range from 7 to 15 years (Texas Parks and Wildlife Department 2015, Turtle Expert Working Group 2000) and I have presumed the middle of that range which is 11 years. The number of eggs laid in the first clutch (Texas Parks and Wildlife Department 2015, Turtle Expert Working Group 2000) should be sufficient to satisfy numerical achievement. The eggs hatch within 55 days (Texas Parks and Wildlife Department 2015) and there is no postnatal care in this species. Thus, my estimated L_r for this species is 11.15 years (11 years plus 55 days). The value of L_r/L_n for this species is 0.279 and the value of $[1-(L_r/L_n)]$ for this species is 0.721, which means that potentially 72 % of this species normal lifetime remains at replacement age.

2.3.3 *Dog (***Canis lupus familiaris***)*

The value that I have used as my estimated average normal longevity, L_n, for this species is 12.67 years, which is equal to 12 years plus 8 months as reported by Michell (1999). It is presumed that the typical age at which females commence breeding is 2 years (value for dingo, Corbett 2004). The first litter produces enough offspring to satisfy numerical replacement presuming there are no losses due to infanticide (Corbett 2004). My estimate of the gestation period is 0.18 years, equal to 65 days, which is the middle point of the 61–69 day range stated by Corbett (2004). Denning typically ends 0.42 years after pups are born, which is equal to 5 months as reported by Boitani and Ciucci (1995), beyond which time the offspring presumably can feed independently. Thus, my estimated L_r for this species is 2.6 years (2 years plus 65 days plus 5 months). The value of L_r/L_n for this species is 0.205 and the value of $[1-(L_r/L_n)]$ for this species is 0.795, which means that typically 79 % of this species normal lifetime remains at replacement age.

2.3.4 *Red-Tailed Hawk (***Buteo jamaicensis***)*

The value that I have used as my estimated average normal longevity, L_n, for this species, is 8.5 years (de Magalhães 2015). Females reach sexual maturity at 730 days (de Magalhães 2015) which is 2.0 years of age. It is presumed that numerical replacement could be achieved with the first clutch of eggs (de Magalhães 2015). The estimated incubation period is 31 days (de Magalhães 2015). The young leave the nest at about 6–7 weeks after hatching but are not capable of strong flight for at least another 2 weeks (National Audubon Society 2015). I have used 45.5 days, equal to 6.5 weeks, as my estimate of the time period required for leaving the nest plus added 2 weeks for the strengthening of flight muscles. Based upon that information, my estimated L_r for this species is 2.25 years (2 years plus 31 days plus 6.5 weeks plus 2 weeks). The value of L_r/L_n for this species is 0.265 and the value of $[1-(L_r/L_n)]$ for this species is 0.735, which means that typically 74 % of this species normal lifetime remains at replacement age.

2.3.5 *House Mouse (***Mus musculus***)*

The value that I have used as my estimated average normal longevity, L_n, for this species is 2 years (Berry 1970). The females reach sexual maturity at 6 weeks (Berry 1970). I have used 5 days as my estimate for their delayed implantation period (Berry 1970). It is presumed that the first litter of offspring satisfies numerical replacement. Gestation typically lasts 3 weeks and is followed by a nursing period of 3 weeks (Berry 1970), after which the offspring can feed independently. Based on that information, my estimated L_r for this species is 0.24 years (12 weeks plus 5 days). The value of L_r/L_n for this species is 0.12 and the value of $[1-(L_r/L_n)]$ is 0.88, which means that potentially 88 % of this species normal lifetime remains at replacement age. The fact that the ratio of L_r to L_n is so dramatically different for this species, as compared to the other example species, is possibly suggestive of the high predation rate typically suffered by this species.

2.4 The Possiblilty of Mathematically Estimating Vital Boundaries

Theoretically, both the inner and outer vital boundaries of a species could be depicted mathematically and calculations approximating conditions just inside the outer vital boundary would have a special application for ascertaining and potentially predicting short term survival for species members under extremely adverse environmental conditions. Importantly, those numerous environmental factors which could serve as variables when defining the potential longevity for members of a species would differ in the extent to which they influence various sections of the inner and outer vital boundary surfaces.

Trying to incorporate all potential variables into such calculations would be as difficult as the challenge faced by the fictional character Hari Seldon, professor of mathematics in Isaac Asimov's Foundation series. Fortunately, the number of variables required to functionally estimate the outer vital boundary and L_t values just inside the outer vital boundary would be relatively fewer than required to estimate the inner vital boundary, because fewer variables can impact life so drastically over extremely short intervals of time. For example, levels of available dietary micronutrients are unimportant if you are dying from hypothermal exposure. Examples of variables that do have importance at the outer vital boundary are ambiental temperature, gases such as oxygen, carbon dioxide, carbon monoxide and chlorine (molecular chlorine), ionizing radiation, certain natural and synthetic toxins including those which have been used for military purposes, and ambiental pressure. In is not necessary for all possible variables to be included in a model. The choice of how many variables need to be included in a given calculation, and which variables those need to be, will depend upon the species and situation being considered.

Figure 2.1 depicts the two concentric theoretical closed surfaces which represent a species inner and outer vital boundaries as polyhedrons. Figure 2.5 delves further into the proposed concept by illustrating the center of a species vital boundary, the species inner vital boundary, and the species outer vital boundary, as points that can be graphed by a plot of relative survival time versus relative distance from the center of the boundary. This distance from the center of the boundary is not a physical measurement, but instead this distance is determined by the parameter values of pertinent environmental variables. The area marked in Fig. 2.5 as 'permanent residence possible' represents the inner boundary region. The area marked in Fig. 2.5 as 'temporary survival possible' represents the interboundary region. The area in Fig. 2.5 marked as 'survival essentially impossible' represents environmental conditions that constitute barriers for the species.

I have represented relative survival time as $\log_{10}L_t/L_n$ for this proposed concept because doing so allows the use of modeling techniques analogous to those procedures developed for modeling microbial population survival versus environmental variables as an exponential decay rate function (Hurst et al. 1980, Hurst et al. 1992). The concepts presented by Hurst et al. (1980, 1992) used ratio values expressed as $\log_{10}N_t/N_o$, in which N_t represented the surviving number of individuals at elapsed time t relative to the number of individuals which had been alive at time 0, with time 0 having been the outset of the observation period, and regressed those ratio values as a dependent variable against time and environmental factors as independent variables. Although analogous, those techniques developed by Hurst et al (1980, 1992) would need to be modified for use with this proposed concept because this proposed concept includes time as part of the dependent variable, relative survival time. In both types of analyses, determining population survival time using ratio values calculated either as $\log_{10}L_t/L_n$ or $\log_{10}N_t/N_o$ requires stating that, during the time period for which the survival is either being observed or

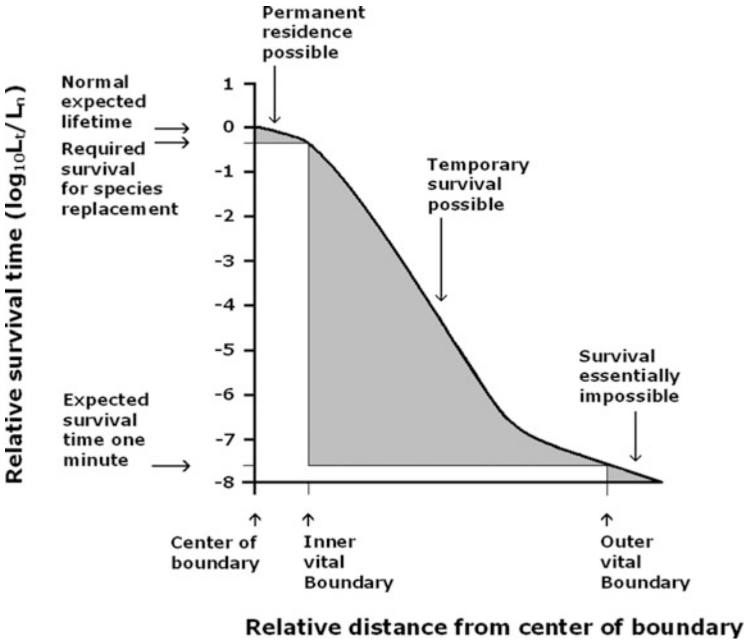

Fig. 2.5 Human relative survival time and boundaries. This figure represents the concept that the relative survival time for some given population of a species, expressed as $\log_{10}L_t/L_n$, will depend upon the parameter values for those environmental variables which are important to the species survival. The favorability of environmental conditions, and thus the expected longevity time (L_t) for members of a species, decreases with outward distance from the center of its vital boundary. By definition, the L_t value which members of a species potentially can achieve at the center of their vital boundary is equal to their normal expected longevity time (L_n) and is their normal expected lifetime under optimum conditions. The inner vital boundary is defined by all combinations of conditions under which expected longevity time would equal the longevity required from birth for members of that species to achieve numerical replacement (L_r). Physical locations where the environmental conditions could allow an expected longevity either equal to or greater than L_r potentially would represent permanent residence locations for that species. The outer vital boundary is defined by all combinations of environmental conditions under which expected longevity time would be one minute. Physical locations where the environmental conditions could allow an expected longevity greater than one minute but less than L_r would allow only temporary survival, thus representing only temporary residence locations, as the conditions in those locations would not allow the species to numerically sustain its population. A species would find its survival essentially to be impossible under any combination of environmental conditions which is beyond that species outer vital boundary, due to the extremely low expected L_t values beyond its outer boundary. Thus, locations where a species L_t would be less than one minute will represent barriers which severely restrict the movement of that species. The curve shown here was not calculated for humans but generally is illustrative of population survival curves

estimated, the environmental conditions remain within statistical limits of the stated parameter values for those environmental factors that are being used as mathematical variables. Thus, for any given species, each possible combination of parameter values for the considered environmental variables would generate a single estimated population survival time, the L_t value for that set of conditions. Only one combination of environmental conditions, the optimum for that species, would yield an L_t value equal to L_n. The surface of the inner vital boundary for that species would be comprised of all combinations of environmental conditions for which the L_t value equals L_r. The surface of the outer vital boundary for that species would be comprised of all combinations of environmental conditions for which the L_t value equals 1 min.

2.4.1 Linear Regression Model

Historically, a presumption has been made that population survival satisfactorily is estimated as a log-linear function (Fig. 2.6) for a given set of environmental conditions. This section of the chapter presents that type of linear modeling approach using a technique developed by Hurst et al. (1980). Their linear regression analyses technique involves two steps, as represented in Fig. 2.7, and was used to examine and model how the survival of viruses in soil was affected by multiple soil characteristics. The general linear model equation is Eq. (2.1).

$$Y = B_0 + B_1 X \tag{2.1}$$

2.4.1.1 Step One of the Linear Regression Technique

The first step in the linear regression technique was done by using Eq. (2.2) to determine the rate of population change, calculated as B_t, for each combination of organism and environmental conditions that had been studied.

$$\log_{10}\frac{N_t}{N_o} = B_0 + B_t t \tag{2.2}$$

2.4.1.2 Step Two of the Linear Regression Technique

The B_t values developed in step one were termed survival slope values, and subsequently used as dependent variable Y for the second step of the analysis. Environmental variables were used as independent variables in the second step of the analysis. Insight was gained by using scatterplots and simple linear regression analysis to examine the relationships between the survival slope values and individual environmental variables using Eq. (2.1). Development of models during the second step of the process was achieved by performing multivariate linear

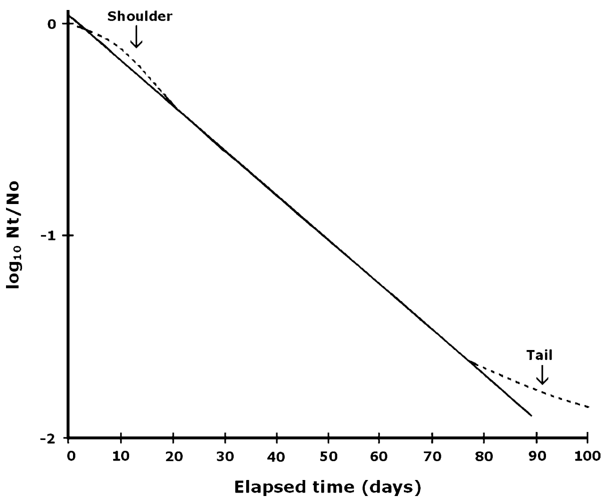

Fig. 2.6 Population survival plot. This is a visual presentation of Eq. (2.2). It illustrates exponential population decay with Log_{10} transformed titer ratio values used as the dependent variable; these values are regressed linearly with respect to time (t) as the independent variable. The *solid line* is the slope, B_t, which represents the rate of population change, or population decay, expressed as $[\log_{10}(N_t/N_o)]/_t$. N_o is the number of population members, or titer if considering a population of microorganisms, existing at time 0 which is the outset of the observation period. N_t is the number of population members, or titer, existing at elapsed time t. B_o is the point where the solid line intercepts the y axis. The dashed lines demonstrate deviations from log linearity that are termed shouldering and tailing. Those deviations reflect the fact that more accurately and precisely modeling population survival requires time to be allowed a coefficient in the form of an exponent as described by Eq. (2.6), which was the basis of the Multiplicative error II equation format developed by Hurst et al (1992)

regression to analyze the survival slope values against a number of different environmental variables using Eq. (2.3).

$$Y = B_0 + B_1X_1 + B_2X_2 + \bullet\bullet\bullet + B_nX_n \tag{2.3}$$

The independent variables, depicted either as X in Eq. (2.1) or as X_1 through X_n in Eq. (2.3), were physical and chemical soil characteristics because that study was designed to assess how soil characteristics determined the survival time of virus populations. Using a backwards elimination regression technique to select which independent variables were to be included in the model equation proved to be the best approach for simplifying the modeling equation, by eliminating as variables those soil characteristics which had least influence upon survival. Once a set of four soil characteristics had been selected as key independent variables, the backwards elimination regression analysis process was repeated several times with the difference being that for each additional trial the regression was run with a single one of the key variables excluded from consideration for incorporation into the multivariate regression equation. Those trials in which variables individually were excluded

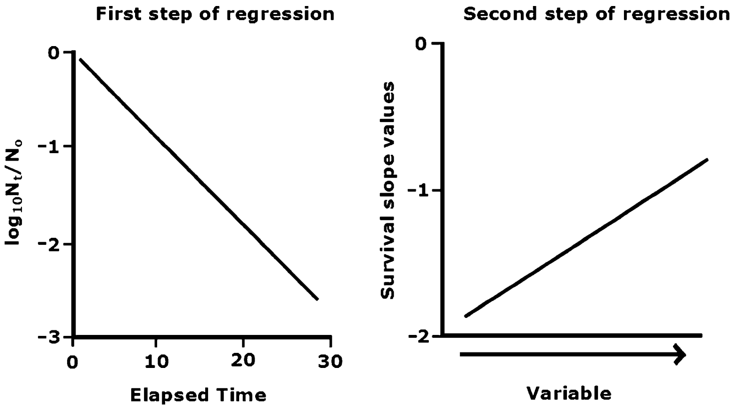

Fig. 2.7 Two step linear regression technique. The first step depicts a survival slope determination which represents Eq. (2.2), with the survival slope values expressed as the rate of $\log_{10}$ numerical change in the population ($\log_{10}N_t/N_o$), termed titer change if considering the survival of microorganisms, per unit time. Those slope values were expressed as [($\log_{10}N_t/N_o$)/time], and the slope values were negative which indicated that the surviving fraction of the population decreased with time. The generated slope values then can be used as the dependent variable in a second regression step, using environmental factors as independent variables to determine the statistical relationship between survival and those environmental factors. This statistical approach initially was developed for studying the survival of viruses with time measured in days, and with the independent variables being temperature and either water or soil characteristics. Equation (2.1) would be used for the second regression step if the choice were to perform simple linear regression, with [($\log_{10}N_t/N_o$)/time] as the dependent variable and a single environmental factor as the independent variable. The basic equation used by Hurst et al. (1980) for that second regression step was Eq. (2.3), with [($\log_{10}N_t/N_o$)/time] incorporated as the dependent variable in a multivariate linear regression which simultaneously examined survival as a function of numerous environmental factors as independent variables. The example shown here for the second regression step represents a positive correlation between the variable and survival, with slope values decreasing as the value of the variable increases. Alternatively, the signs of both the slope values and the *y*-axis intercept from the first step of the regression can be inverted, and then termed inactivation rate values rather than slope values, before regressing those slope values as dependent variable against environmental factors as the independent variables. If this type of mathematical approach were used for modeling survival, i.e., L_t, as the dependent variable against environmental factors as independent variables, then only the second step of the regression technique would be used with $\log_{10}L_t/L_n$ values substituted as dependent variable in place of $\log_{10}N_t/N_o$ values, and consequently the modeling equations could not use time as an independent variable since longevity expressed as either L_t, L_n, or L_r already incorporates time. This figure has been redrawn from Hurst et al. 1980

helped with understanding the interrelationships between the four key characteristics. The final model equation incorporated all four key characteristics as independent variables, and we better understood the role of each characteristic.

2.4.1.3 Adapting the Two Step Linear Regression Technique for Use with Longevity Values

Using the backwards elimination approach (Hurst et al. 1980) for evaluating the relative importance and interactions between environmental factors as pertaining to vital boundary conditions would require eliminating their first step which utilized Eq. (2.2), and instead directly proceeding to Eq. (2.3) with the values of $\log_{10}L_t/L_n$ used as Y. The reason for modeling vital boundary conditions by using just the second step of the Hurst et al. (1980) procedure, is that production of the slope values during the first step of their analysis utilized change in titer represented by $\log_{10}N_t/N_o$ for the dependent variable with time incorporated as an independent variable. The slope values generated from Eq. (2.2) thus represented change per unit time as $[(\log_{10}N_t/N_o)/\text{time}]$, and usage of those slope values as dependent variable during the second step of the regression technique then placed time on the dependent side in Eq. (2.3). The values of $\log_{10}L_t/L_n$ already incorporate time, and since time should not be used on both sides of an equation, it would be appropriate to use only the second step of their two step analysis technique. Equation (2.4) will be the result from using $\log_{10}L_t/L_n$ as the dependent variable for this type of modeling approach.

$$\log_{10}\frac{L_t}{L_n} = B_0 + B_1X_1 + B_2X_2 + \bullet\bullet\bullet + B_nX_n \tag{2.4}$$

2.4.2 Non-Linear Regression Model

The study by Hurst et al. (1992) compared how well eight different equation formats served for developing regression models to understand the survival of viruses in environmental water. Their approach was to regress common sets of experimentally determined N_t/N_o survival ratio values as dependent variable versus a predetermined set of water characteristics as independent variables. The models generated using those different equation formats, along with their respectively calculated coefficients, then were used to predict what the outcome from that study should have been. Predictions were made both for the same parameter value ranges that had been used to generate the models, and also for parameter value ranges beyond those that had been used to generating the models. Then, the sets of values predicted by each of the different modeling equation formats were compared by simple regression against the actual experimentally observed values. The best equation format proved to be one based upon the general non-linear Eq. (2.5):

$$Y = B_0 X_1^{B_1} X_2^{B_2} \bullet \bullet \bullet X_n^{B_n} \tag{2.5}$$

with N_t/N_o used as the dependent variable Y. Time was used as one of the independent variables. Following linearization the result was Eq. (2.6), which the authors termed their Multiplicative error II equation format.

$$\begin{aligned} \log_{10}\frac{N_t}{N_o} &= \log_{10}B_0 + B_1\log_{10}X_1 + B_2\log_{10}X_2 \\ &\quad + \bullet\bullet\bullet + B_n\log_{10}X_n + B_t\log_{10}t \end{aligned} \tag{2.6}$$

Importantly, the Multiplicative error II equation format demonstrated the greatest ability to accurately predict survival under parameter value ranges beyond those for which the coefficients had been developed. It also showed that time requires a coefficient in the form of an exponent.

2.4.3 *My Best Suggestion for Mathematically Estimating Vital Boundaries*

Either the linear or non-linear regression approach could be used for developing modeling equations to analyze and predict vital boundary conditions. My best suggestion would be to use Eq. (2.7) as the starting point, which would be analogous to the Multiplicative Error II equation format but with relative survival time substituted as the dependent variable and time deleted from the independent side of the equation.

$$\begin{aligned} \log_{10}\frac{L_t}{L_n} &= \log_{10}B_0 + B_1\log_{10}X_1 + B_2\log_{10}X_2 \\ &\quad + \bullet\bullet\bullet + B_n\log_{10}X_n \end{aligned} \tag{2.7}$$

2.5 Relating This Concept to the Process of Evolution and the Niche of a Species

Evolution is a process which attempts to maximize usage of available energy resources by the development of species. Each evolved species has an ecology which we can define as including two main aspects. One of these aspects is the collective set of actions and functions performed by that species, by which we define the species niche. Another aspect is the established range of environmental conditions under which this species can survive. Physical locations which meet the requirements for that range of environmental conditions define the potential habitat areas within which this species can reside.

Which came first, the habitat or the niche? Posing this question leads us to a cyclical process of understanding. My personal guess would be the habitat, because no species can function without a location capable of supporting life. And yet, the opportunities and requirements of a niche help to establish the range of environmental conditions in which the occupying species will reside. Evolution therefore is a reactionary process that must establish both the niche and environmental requirements of a species simultaneously. By studying the ways in which the habitat of an individual species overlaps, and its niche interconnects, with those of other species, we can gain an understanding of the evolutionary path that consequently produced the observed species. That path will have led the species to an eventual success which may be either long term or simply a quick demise.

Once a species has evolved in response to selection pressures, the species becomes constrained in ways that we can define both with regard to the set of environmental conditions under which the species successfully can reside, which is the purpose of the habitat definition concept presented in this chapter, and also with regard to its niche (Hurst 2016). My hope in presenting this habitat definition concept is that it may prove to be a helpful tool, but that success depends upon the possibility of someone recognizing this concept as being useful. Unless it finds utility, the fate of this concept will be just that of an unused wrench which can serve as little more than either a paperweight or doorstop. But then, I own a set of wrenches that seldom get used.

2.6 Some Questions and Answers Regarding This Concept

Why the choice of 1 min for the outer vital boundary? The mathematical distance from the center of the boundary outward would be infinite, and correspondingly the value of $\log_{10}L_t/L_n$ approaches its minimum value as an asymptote. It therefore is necessary to pick some L_t value as representing a practical minimum duration of survival. The choice of 1 min was not entirely random, but did seem to represent a practical choice.

Are there more than just two boundaries? There actually would be an enormous number of theoretical closed surfaces layered as concentric shells between the center of a species boundary and its outer vital boundary, with each possible L_t value which is less than L_n representing a different shell. L_n itself represents a single point. As an example, my L_n value for humans is 67.1 years and if L_t were estimated in units of minutes, then for humans there would be 35,291,915 concentric shells [(67.1 years × 365.25 days per year × 24 h per day × 60 min per hour) – 1]. That minus 1 represents the center point, L_n. Six of those shells are identified in Table 2.3, and they are: $L_t = L_r$, $L_t = 1$ year, $L_t = 1$ month, $L_t = 1$ day, $L_t = 1$ h, and $L_t = 1$ min. I have designated two of those shells as perhaps representing the more significant demarcations from the perspective of a species survival, and termed those two shells as the inner and outer vital boundaries.

Where would L_{max} fit into this concept? Each L_t value would consist of a designated average value and include a statistical deviation range. As an example, I have used 67.1 years as my L_n for humans which is the reported world value for life expectancy at birth (United Nations 2013). L_{max}, which would be the maximum normal lifetime for members of a species, marks the upper limit of the species L_n range. The L_{max} for humans is approximately 114 years.

Are there other usages for the concept of L_t/L_n ratio values? It would be possible to develop L_t/L_n data for subgroups of a species and valuable comparative information could be gained in that way. When we consider either animals or plants, those groupings might be based upon subspecies with an example being that different breeds of dogs vary in their life expectancy. Subgroupings for humans might be based upon their location of residence, such as by country, and valuable demographic information could be gained in that way. These other usages of L_t/L_n ratio values are a departure from the concept of vital boundaries. As mentioned earlier, although it is not possible to determine a value of L_t/L_n that represents L_r for Japan alone since the human population in that country currently does not achieve numerical replacement, we can assess a value of L_t/L_n at the time of first human birth for Japan and the value would be 0.37 (30.3 years divided by 81.8 years). This value of 0.37 indicates that on average the first childbirth in Japan occurs when 37 % of a womans lifetime has passed, and she then has 63 % of her lifetime remaining. The corresponding number would be 0.48 for Sierra Leone (19.2 years divided by 40.1 years) indicating that on average the first human birth in Sierra Leone occurs when 48 % of a womans lifetime has passed, and then 52 % of her lifetime remains. Comparing those calculations for Japan versus Sierra Leone tells us that although the first human birth for women in Japan comes at a later age of 30.3 years rather than 19.2 years, that first human birth for Japanese women comes at a relatively earlier point when considered from the perspective of a womans average life expectancy.

How can we understanding the vital boundaries of a virus? Virus are one of the special cases in biology because of their nature as obligately intracellular parasites that lack metabolic activity outside the confines of a host cell. And for many, the issue of “Is a virus even alive?” further complicates the discussion. So, how could we really define the vital boundaries for a virus, as its boundaries would seem to change depending upon whether the virus is inside a host cell or resting dormant on a surface somewhere? We know that the vital boundaries of a virus would seem to be heavily defined by its host because a virus exhibits metabolic “life” only within either a permissive or semipermissive host cell. We even know that retroviral DNA apparently can be incorporated permanently into the host genome, at which point the virus and its host have the same biological agenda and symbolically have joined to create a single species (Hurst 2011). The hypovirulence elements of the fungi which cause Chestnut blight disease are another clue, these elements apparently evolved from a virus and have achieved symbiosis with their fungal host to such an extent that often the fungus seems unable to have permanent survival in nature without its viral-derived symbiont. These hypovirulence elements sustain their existence by reducing virulence of their host fungi so that the host fungus does not kill the tree upon which the fungus feeds, enabling survival of the hypovirulence element, fungus and tree. It thus would seem that the vital boundaries of the virus evolutionarily have changed by conforming to the vital boundaries of their infected hosts, and this is particularly true both for those virus species which have become symbiotic and also for many of the viral-derived elements. The vital boundaries of a virus species therefore would be represented by the vital boundaries of its infected host. The inner vital boundary of the virus would be the outer vital boundary of a permissive host. The outer vital boundary of the virus would be the outer vital boundary of a semipermissive host. Mathematically modeling the survival of a species population, such as animals, under defined environmental conditions actually represents modeling the rate at which members of that population die by becoming metabolically inactive and is the function of L_t values and L_t/L_n values presented in this chapter. Virus particles are by themselves metabolically inactive, and mathematically modeling the survival of a virus population using N_t/N_o values actually represents determining not the rate at which virus die, but rather the rate at which virus lose their ability to be revived.

How to model the fate of bacterial endospores? Bacterial endospores, like virus particles, are metabolically inert survival structures. Nonenveloped virus particles have a notable environmental robustness and are capable of reactivating after decades of appropriate storage. Bacterial endospores have an even more amazing capability for environmental stability that extends for perhaps 25 million years (Cano and Borucki 1995). Both virus particles and bacterial endospores function by protectively allowing genetic material to survive in a revivable form under environmental conditions which are too extreme for allowing their species to demonstrate metabolic activity. Both bacterial endospores and virus particles also aid the dispersal of their species in addition to aiding their species survival. There certainly are notable morphological differences between these two types of metabolically inert survival structures. It also is important to remember that production of virus particles is a reproductive strategy which generates numerous virus particles per host cell, in contrast with the fact that endospore production is not reproductive and instead yields a ratio of only one spore per vegetative cell. Equations (2.4) and (2.7) could be used for modeling the vital boundaries of bacterial species when their cells are in a metabolically active vegetative state, in just the same manner as those equations would be used for modeling the vital boundaries of the animals which have been presented as example species for this publication. It would be appropriate to model the persistence of bacterial endospores by using the concept of $\log_{10}N_t/N_o$ ratio values and the analysis techniques presented by Hurst et al. (1980, 1992) which included Equations (2.2) and (2.6), and thereby assess the rate at which the spores lose their capacity for revitalization just as done for modeling population decay rates of virus particles. It also would be appropriate to model the persistence of either lyophilized or cryopreserved vegetative cells using the concept of $\log_{10}N_t/N_o$ ratio values and the analysis techniques presented by Hurst et al. (1980, 1992) which included Eqs. (2.2) and (2.6), because both lyophilized as well as cryopreserved cells are being held in a metabolically inactive state under environmental conditions beyond the outer vital boundary of their species.

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