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Forum

Definitions of pathogenicity and virulence in invertebrate pathology

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Abstract

Accurate definition and usage of terminology are critical to effective communication in science. In a recently published article, the clarity and consistency of the terms pathogenicity and virulence as used in invertebrate pathology were called into question, and a revision of these terms was proposed. Our objective was to examine definitions of pathogenicity and virulence and their use in invertebrate pathology, and respond to this article. Although usage of the terms pathogenicity and virulence varies, we found considerable consistency in the published definitions of these terms in the invertebrate pathology literature throughout the history of the discipline, as well as among related disciplines such as medicine and microbiology. We did not find the established definitions to be lacking in clarity or utility. Therefore, we recommend that the definition and use of these terms adhere to precedence. Specifically, pathogenicity is the quality or state of being pathogenic, the potential ability to produce disease, whereas virulence is the disease producing power of an organism, the degree of pathogenicity within a group or species. Pathogenicity is a qualitative term, an "all-or-none" concept, whereas virulence is a term that quantifies pathogenicity.

Keywords: Definition; Pathogenicity; Virulence; Terminology

1. Introduction

Communication is central to the advancement of science. Effective scientific communication is facilitated by terminology that is clearly defined and properly used. Casadevall and Pirofski (1999) point out that terminology may change as science evolves; for example, the concepts of pathogenicity and virulence have been affected by major strides in pathology such as the revelation of Koch's postulates and the intricacies of immune response. Changes in terminology due to advances in science are justifiable and necessary. However, if motivations to alter terminology are not based on scientific progress, then it is generally best to avoid change and rely on precedence for accurate definitions. Frequent alterations in terminology are likely to lead to confusion. The motivation to alter terminology may also lie in a lack of clarity or consistency, in which case clarity must be sought and a solution proposed. To achieve clarity, it is best to avoid changing concepts in terminology more than necessary. The solution should be based on precedence and unifying concepts within the literature used in the discipline.

Varying definitions and uses of the terms pathogenicity and virulence have been a topic of discussion among several disciplines in the field of pathology (Andvrivon, 1993; Bos and Parlevliet, 1995; Casadevall and Pirofski, 1999; Shaner et al., 1992; Thomas and Elkinton, 2004; Watson and Brandly, 1949). In a recent

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article, Thomas and Elkinton (2004) found that confusion exists within the discipline of invertebrate pathology over the definitions of pathogenicity and virulence. They argued that confusion arose from a lack of consistency and clarity of use within the field of invertebrate pathology, as well as among other disciplines such as evolutionary biology, medicine, microbiology, and plant pathology. To provide greater consistency, Thomas and Elkinton (2004) proposed a revised definition that is formula driven: pathogenicity (# dying/# exposed) = infectivity (# infected/# exposed) × virulence (# dying/# infected). They defined infectivity as the ability of a pathogen to enter the host, and spread, and/or reproduce within that host. These definitions are not intended to be based solely on mortality, but can also be extended to other manifestations of disease such as fecundity and toxin production.

As individuals representing a diversity of the subdisciplines of invertebrate pathology, this paper presents our position on the definitions of pathogenicity and virulence and responds to the issues raised by Thomas and Elkinton (2004).

2. Definitions of pathogenicity and virulence

Definitions for pathogenicity and virulence from Thomas and Elkinton (2004) and from notable invertebrate pathology texts are provided in Table 1. The glossary by Steinhaus and Martignoni (1970) is a revised version of their first glossary of terms in invertebrate pathology, and thus should be considered the definitive work of precedence. We think Steinhaus and Martignoni's (1970) definitions of pathogenicity and virulence are clearly distinguishable and remain useful to today's science. Therefore, these definitions should be adhered to within the discipline of invertebrate pathology. Restated, pathogenicity is the quality or state of being pathogenic, and virulence is the disease producing power of an organism, i.e., the degree of pathogenicity within a group or species. Although the definitions in invertebrate pathology subsequent to Steinhaus and Martignoni's (1970) are not all completely identical there is substantial consistency among them (with the exception of Thomas and Elkinton (2004)) (Table 1). In essence, each definition does not depart from the original. Typically, all definitions, aside from those of Thomas and Elkinton (2004), indicate pathogenicity as the more general (qualitative) term and virulence as a measure (i.e., the degree) of pathogenicity. Additionally, in some invertebrate pathology texts pathogenicity and virulence are not defined explicitly, e.g., Lysenko (1963). Nevertheless, it is clear from the manner in which the authors distinguish the terms that the concepts are consistent with the definitions listed in Table 1. For a given host and pathogen, pathogenicity is absolute whereas virulence is variable, e.g., due to strain or environmental effects. Pathogenicity is an all-or-none phenomenon. An organism is either pathogenic to a host or it is not. In contrast, virulence is a measurable characteristic of the ability to cause disease. In general, pathogenicity is applied to groups or species, whereas virulence is intended for within group or species comparisons. However, both terms can conceivably apply to a "group" at or across any taxonomic

Table 1
Definitions of pathogenicity and virulence in invertebrate pathology texts in comparison to those of Thomas and Elkinton (2004)

Reference	Pathogenicity	Virulence
Steinhaus and Martignoni (1970)	The quality or state of being pathogenic. The potential ability to produce disease	The disease producing power of an organism. Degree of pathogenicity within a group or species
Aizawa (1971)	… the ability of a strain or species of micro-organism to produce disease in various hosts. Indicates term is used qualitatively	Degree of pathogenicity against a specific species host in controlled conditions within a group or species of microorganisms. Indicates term is used quantitatively
Cantwell (1974)	The quality of being pathogenic	The quality of being virulent; the quality of being poisonous; the disease producing power of a microorganism
Tanada and Fuxa (1987)	The ability to invade and injure the host's tissues. Applies to groups or species of pathogens	The disease producing power of the pathogen, the ability to invade and injure the host's tissues. The degree of pathogenicity within a group or species
Tanada and Kaya (1993)	Nearly synonymous with virulence but applied to groups or species	The disease producing power of a microorganism. The ability of a microorganism to invade and cause injury to the host. The relative capacity of a microorganism to overcome the host defense mechanisms… The degree of pathogenicity within the group or species
Lacey and Brooks (1997)	The quality or state of being pathogenic. The potential ability to produce disease. Applied to groups or species	The disease producing power of an organism. Degree of pathogenicity within a group or species
Thomas and Elkinton (2004)	The number of dead individuals relative to the number exposed to the pathogen	The number of dead individuals relative to the number infected

level (strain, species, family, etc.), provided that pathogenicity is qualitative and virulence is a comparative measure. Here we provide a few examples. The *Agrotis ipsilion* nucleopolyhedrovirus (AgipMNPV) is more virulent to the black cutworm, *Agrotis ipsilon* (Hufnagel) than the *Autographica californica* nucleopolyhedrovirus (AcMNPV) (Boughton et al., 1999). The nematode–bacterium complex *Steinernema carpocapsae* (Weiser) has been reported to show pathogenicity to some non-insect arthropods such as certain ticks (Samish et al., 2000), but not mammals, e.g., rats (Gaugler and Boush, 1979). Lastly, the GA3 strain of *Beauveria bassiana* is pathogenic to the pecan weevil, *Curculio caryae* (Horn), but is not as virulent to this host as the MS1 strain (Shapiro-Ilan et al., 2003).

Operational definitions are useful in identifying empirical approaches to determine whether an organism fits the criteria of pathogenicity and virulence. Pathogenicity can be operationally defined as meeting Koch's postulates. When addressing pathogenicity with Koch's postulates, however, it should be kept in mind that some organisms are opportunistic (generally incapable of invading the host of their own accord), or will only cause disease when combined with other organisms. Therefore, some description of the conditions under which Koch's postulates would be met may be warranted when discussing pathogenicity for certain organisms. Virulence can be operationally defined in a broad sense by any observable measure of disease severity or degree. Measures of disease severity are often associated with dose-response assessments of mortality such as LD_{50}, LC_{50}, lethal times, but may also include single dose mortality assays, or non-lethal measures, e.g., ET50, reductions in fitness, or extent of tissue damage.

Definitions of pathogenicity and virulence as used in invertebrate pathology are highly consistent with those found in some major texts and treatises in other disciplines, particularly in medicine and microbiology (Table 2). For example, consistency is found in microbiology texts (Dubos, 1945; Ford, 1927), prominent texts of medical terminology (Dorland's, 2003; Stedman's, 2000; Taber's, 2001), and proposed definitions based on an extensive review of literature pertaining to microbial pathogenesis (Casadevall and Pirofski, 1999). As in invertebrate pathology, the medical and microbiology definitions listed in Table 2 indicate pathogenicity to be a more general or qualitative term referring to the ability to cause disease, whereas virulence is a relative term describing the degree or strength of pathogenicity.

In contrast, definitions of pathogenicity and virulence in plant pathology vary considerably within the discipline and often diverge from definitions in invertebrate pathology. Reviews by Bos and Parlevliet (1995) and Shaner et al. (1992) point out substantial divergence in plant pathology definitions of pathogenicity and virulence. For example, the definitions used in invertebrate pathology appear quite compatible with the definitions of Agrios (1988), but are almost opposite to the definitions of Bos and Parlevliet (1995), which describe pathogenicity as the quantitative term and virulence as qualitative (Table 2). Thomas and Elkinton (2004) indicate that many authors in plant pathology (45–50% in a survey of papers in plant pathology journals) depart from the invertebrate pathology definition by viewing

Table 2
Definitions of pathogenicity and virulence in various disciplines

Discipline	Reference	Pathogenicity	Virulence
Medicine (pathology/ cytology)	Young and Barger (1971)	The ability of an organism to cause disease	The severity of an infection. It quantitates pathogenicity
Medicine	Stedman's Medical Dictionary (27th edition, 2000)	The condition or quality of being pathogenic, or the ability to cause disease	The disease evoking severity of a pathogen
Medicine	Taber's Cyclopedic Medical Dictionary (19th edition, 2001)	The state of producing or being able to produce pathological changes and disease	The relative power and degree of pathogenicity possessed by organisms
Medicine	Dorland's Illustrated Medical Dictionary (30th edition, 2003)	The quality of producing or the ability to produce pathological changes or disease	The degree of pathogenicity of a microorganism as indicated by the severity of the disease produced and its ability to invade the tissues of a host
Microbiology (bacteriology)	Ford (1927)	Ability of the infectious organism to invade the organs and tissues	The strength of their [bacteria's] pathogenic activity… the sum of their disease producing properties
Microbiology/ microbial pathogenesis	Casadevall and Pirofski (1999)	The capacity of a microbe to cause damage in a host	The relative capacity of a microbe to cause damage in a host
Plant pathology	Shaner et al. (1992)	Comprehensive term to refer to the ability of a microorganism to cause disease	Relative capacity to damage the host
Plant pathology	Bos and Parlevliet (1995)	Quantitative capacity to cause disease; the overall disease inducing capacity of a biotic or abiotic factor	Ability of a parasite to incite reaction and cause disease
Plant pathology	Agrios (1988)	The capability of a pathogen to cause disease	The degree of pathogenicity of a given pathogen

virulence as a qualitative term. Furthermore, unlike invertebrate pathology definitions (and similar to those proposed by Thomas and Elkinton), recent plant pathology definitions tend to view the ability to invade and reproduce within a host as a separate concept from that of virulence (Bos and Parlevliet, 1995; Shaner et al., 1992). The issue of separating ability to invade from virulence is addressed later in more detail.

Previous reviews (Casadevall and Pirofski, 1999; Shaner et al., 1992) have noted that differences in understanding pathogenicity and virulence may be expected among scientists who study different pathogen groups. Differences might also be expected among scientists studying different hosts such as animals versus plants. This may explain some of the differences between the use of these terms in plant pathology and invertebrate pathology. Emphasis and methodology between the disciplines differ. For example, plant pathologists are less likely to use the concept of lethal dose (i.e., LD_{50}) or lethal concentration (i.e., LC_{50}) in assessing pathogen effects on a host. We conducted a survey of abstracts in ISI Current Contents Connect for two plant pathology journals (*Plant Disease* and *Phytopathology*) and the *Journal of Invertebrate Pathology* to determine the number of papers from December 1997 to May 1998 that used LD_{50} or LC_{50}. In the plant pathology journals, only three out of 2811 papers (0.1%) listed LD_{50} or LC_{50} in the abstract or title. And none of these used the method to assess pathogen effects on the host (rather the assays were used to assess effects of chemicals on the pathogens, or the effects of pathogens on non-target animals). In contrast, in the *Journal of Invertebrate Pathology* 31 out of 568 (5.5%) abstracts indicated that LD_{50} or LC_{50} was used to assess pathogen effects on the host.

Although definitions of pathogenicity and virulence among invertebrate pathology texts appear to be reasonably consistent, usage of these terminologies in invertebrate pathology papers is not consistent. Thomas and Elkinton (2004) reported variation in terminology usage in papers published in the *Journal of Invertebrate Pathology* between 1992 and 2002. We surveyed abstracts in the *Journal of Invertebrate Pathology* between January 1998 and May 2004 (Table 3), and found that, based on the definitions of Steinhaus and Martignoni (1970), the terms pathogenicity or virulence were used incorrectly in 34% of the articles. The most common error was using the term pathogenicity in place of virulence (30%) (Table 3). In this regard, the concern expressed by Thomas and Elkinton (2004) is valid.

3. Response to Thomas and Elkinton (2004)

We think that Thomas and Elkinton (2004) did not provide a complete or accurate representation of definitions for pathogenicity and virulence in invertebrate pathology, and that a number of arguments made against the use of these definitions in invertebrate pathology were erroneous or flawed. For example, the authors state "insect pathologists typically equate virulence with LD_{50}." More accurately, insect pathologists typically use LD_{50} as a measure of virulence. Thomas and Elkinton (2004) also erred in indicating that Fuxa and Tanada (1987a) defined pathogenicity and virulence as synonyms. Moreover, Thomas and Elkinton (2004) did not report definitions of pathogenicity and virulence from the text of Burges and Hussey (1971) or Cantwell (1974). Furthermore, when citing definitions from the relatively recent text, Lacey (1997), it appears that Thomas and Elkinton (2004) overlooked the glossary (Lacey and Brooks, 1997), where the definitions are identical to those of Steinhaus and Martignoni (1970).

Thomas and Elkinton (2004) suggest that confusion between the terms pathogenicity and virulence can be solved through a hierarchical arrangement of terms. The established definitions in invertebrate pathology, however, already encompass a hierarchy. Pathogenicity encompasses virulence and is the more general term. Pathogenicity is a prerequisite of virulence. Virulence cannot be measured in an organism that is not pathogenic, and if an organism is virulent, then it must also be pathogenic.

Thomas and Elkinton (2004) argue against a qualitative nature (i.e., the "all-or-none" concept) in the term pathogenicity. They state that useful definitions of pathogenicity and virulence must yield explicit ways to measure them. This concept is erroneous for pathogenicity. There is no requirement that a scientific term be quantitatively measurable in order to be useful. There are numerous examples of terms in invertebrate pathology that do not "yield explicit ways to measure them" but are useful nonetheless, such as (taken from Steinhaus and Martignoni, 1970) aphagia (inability to ingest), axenic (free from associated organisms), cytocidal (that which kills cells), diagnosis (to distinguish one disease

Table 3
Survey of usage for terms pathogenicity and virulence in Journal of Invertebrate Pathology[a]

Correct usage			Incorrect usage		
Virulence used correctly	Pathogenicity used correctly	Both terms used correctly	Virulence used in place of pathogenicity	Pathogenicity used in place of virulence	Both misused or other error
27	3	3	0	15	2

[a] 50 Titles and abstracts containing the terms pathogenicity or virulence were reviewed from issues 71(1) January 1998 to 85(2) February 2004.

from another), and entomophagous (insectivorous). Clearly, a term does not need to be measurable. A term must simply be observable or detectable in some manner and be descriptive enough to communicate a clear and unique concept.

Moreover, Thomas and Elkinton (2004) propose that the term virulence only applies to individuals that are already infected (where infectivity includes invasion and spread or reproduction of the pathogen within the host). They suggest that infectivity is a completely separate concept from virulence. Their proposal is in contrast to the microbiology and invertebrate pathology definitions that take precedence. The early microbiology literature that we consulted clearly includes infectivity as a component of virulence (Dubos, 1945; Ford, 1927; Watson and Brandly, 1949). In defining virulence, Dubos (1945) writes "it is clear that the ability of a microorganism to establish a pathological state in a given host is the summation of a number of different and independent attributes such as communicability, invasiveness, toxigenicity, etc." Subsequent reviews on pathogenicity and virulence terminology such as one published in *Annual Review of Microbiology* by Watson and Brandly (1949), and another by Casadevall and Pirofski (1999), concur with Dubos's conception of virulence. The historical view in the invertebrate pathology literature also clearly indicates that entrance into the host is a component of virulence, whether directly by the microorganism itself or indirectly by toxins produced by a microorganism in the gut. Steinhaus (1949) states that virulence is "the ability of a microorganism to invade and injure the tissues or body of the host". This view is reiterated in subsequent invertebrate pathology texts (e.g., Tanada and Fuxa, 1987; Tanada and Kaya, 1993).

Thomas and Elkinton (2004) want to use the terms pathogenicity and virulence in a theoretical analysis of pathogen evolution. Similar to their predecessors Anderson and May (1982), they require a simple model that includes several rigorously defined processes. However, modelers and theorists may not be the best group to look to for practical definitions that satisfy the broad needs of the scientific community. For instance, Anderson and May (1982) defined both pathogenicity and virulence as disease-induced mortality. As Onstad (1992) pointed out, operational definitions of important terms are often missing from epizootiological theories created by modelers.

Thomas and Elkinton's (2004) particular difficulty with the terminology stems from their studies involving an evolutionary tradeoff between transmissibility and virulence. They define transmissibility as a component of infectivity, i.e., the ability to enter the host (incidentally, this definition is also erroneous; infectivity is actually a component of, and the final step in transmission (Fuxa and Tanada, 1987b)). The authors suggest that one cannot discuss a tradeoff between virulence and transmission if transmission is a component of virulence. Their problem is understandable. However, as we noted above, the ability to directly or indirectly enter the host is indeed a component of virulence according to precedence in invertebrate pathology and microbiology. Alteration of existing (and useful) terminology to suit a particular series of studies is unwarranted. Thus, rather than change existing terminology, we suggest the necessary concepts be conveyed with a more detailed or delimited utilization of current terminology. If that is not feasible, then new terms should be developed. In Thomas and Elkinton's case, new terminology is not necessary. Their proposed definition of virulence (# dying/# infected) is in fact synonymous with a concept that already exists in invertebrate pathology, i.e., case-fatality rate (Fuxa and Tanada, 1987b). Therefore, the authors could accurately describe their concept as "a tradeoff between transmission and case-fatality rate" (or in cases where mortality is not the measure of virulence, "a tradeoff between transmission and virulence once inside the host").

Even if redefinition of pathogenicity and virulence were warranted, the terminology proposed by Thomas and Elkinton (2004) would be impractical. In measuring the ability of an organism to cause disease, invertebrate pathologists rely heavily on estimating mortality of the host, e.g., through LD_{50}, LC_{50}, lethal times, use of single distinguishing dosages, etc. Thomas and Elkinton (2004) conclude that mortality assessments involving external exposure of the host to the pathogen are measures of pathogenicity because they include infectivity (entry, establishment, and spread of the disease agent); this assessment is consistent with their proposed definitions. Further, the authors contend that mortality assessments involving injection of the pathogen into the host are "more of a measure of virulence rather than pathogenicity, although [they] still involve establishment and spread within the host and thus infectivity as well as virulence." The previous statement illustrates the problematic nature of the proposed definitions. The authors strive to distinctly separate the terms pathogenicity, infectivity, and virulence, but in practical application it is apparent that overlap is to be expected. To truly adhere to the definitions proposed by Thomas and Elkinton's (2004), all bioassays in which only mortality is assessed (including injection assays) would be considered measures of pathogenicity; virulence, according to their definition, cannot be measured unless infectivity is empirically determined.

To overcome the problem Thomas and Elkinton (2004) suggest "for many invertebrate pathogens, bypassing the integument almost assures that the pathogen will become established. The closer this probability is to one the closer an injection bioassay measures virulence." The suggestion invites error and imprecision in distinguishing between pathogenicity and virulence. For example, some organisms may cause severe disease when artificially injected, but are incapable of invading on their own and therefore are not truly pathogenic (Bucher, 1963). Also, one cannot assume that pathogens that enter the host automatically become established—it is simply not the case (Dunphy and Thurston, 1990; Tanada and Kaya, 1993; Watanabe, 1987). Furthermore, even if one did assume that all pathogens that bypass the host integument became established, the mortality measurement would not clearly fit Thomas and Elkinton's definition of virulence in lieu of their definition of pathogenicity. The two would be identical (if # infected/# exposed = 1, then # dead/ exposed = # dead/# infected).

The fact that infectivity (# infected/# exposed) is not easily measured exacerbates the problem. To obtain a truly accurate measure of infectivity the presence of pathogens would have to be determined in all hosts (live and dead). Thomas and Elkinton (2004) suggest that the presence of pathogens in live hosts might be accomplished through DNA probes, but clearly this would not be a practical approach for numerous studies that are aimed simply at assessing relative pathogen effects on host mortality (e.g., most evaluations of LC_{50}, LD_{50}, etc.). Adoption of Thomas and Elkinton's (2004) proposed terminology, and the associated difficulty in separating or measuring infectivity, would inherently lead to diminished utility in the term virulence.

4. Conclusion

We commend Thomas and Elkinton (2004) for addressing the issue of how the terms pathogenicity and virulence are used within the field of invertebrate pathology. Certainly, the topic requires attention. We concur with Thomas and Elkinton (2004) that usage of the terms pathogenicity and virulence has varied in invertebrate pathology literature, and thus steps should be taken to overcome the problem. Perhaps more widespread exposure to the terminology of invertebrate pathology in relevant graduate courses would contribute to achieving consistency. Although full-length courses in invertebrate pathology have declined over the years, expansion of short courses and incorporation of invertebrate pathology into more general courses such as Biological Control and Integrated Pest Management can offer additional venues for instruction in terminology. Additionally, in concurrence with Thomas and Elkinton (2004), we suggest that communication in science can be improved by including definitions of terms, where necessary, in research articles and especially in review papers.

In contrast to Thomas and Elkinton (2004), we found the definitions for pathogenicity and virulence in invertebrate pathology to be clearly distinct and useful. The definitions have been based on precedence, and have exhibited considerable consistency within the discipline and among several related disciplines. We conclude that Thomas and Elkinton's (2004) arguments against traditional definitions in invertebrate pathology are not sound or sufficient enough to warrant revision. Additionally, we found the revised definitions proposed by these authors to be problematic and impractical. We recommend adhering to invertebrate pathology's established definitions of pathogenicity and virulence as defined by Steinhaus and Martignoni (1970) and described above. We further recommend that Steinhaus and Martignoni (1970) be considered the definitive work on terminology for invertebrate pathology, and that the possibility of republication be explored.

We realize that in biology, all bioassays, hypotheses, models, and terminology are simple representations of nature that typically aggregate complex processes. For example, our concept of virulence is an aggregation of various factors that contribute to causing harm to a host. There is no way to prevent biologists from aggregating or disaggregating their scientific concepts or methods in different ways. We can only encourage each scientist (and each editor) to take responsibility in striving for consistency and clarity when conveying concepts and methodology in the scientific literature.

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