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INFECTIOUS DISEASE ECOLOGY AND CONSERVATION

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This book is dedicated to the countless field conservation biologists and wildlife veterinarians who struggle daily, often at great personal cost, for the protection of the planet's biodiversity. It is also dedicated to the present generation of students whose idealism and energy make us hopeful that a better world is within reach.

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List of Acronyms and Abbreviations

ACE-2	angiotensin-converting enzyme 2
AIC	Akaike information criterion
ANOVA	analysis of variance
bTB	bovine tuberculosis
CM	capture myopathy
CSF	classical swine fever
CWD	chronic wasting disease
CyHV-3	cyprinid herpesvirus-3
DRA	disease risk analysis
ELISA	enzyme-linked immunosorbent assay
ESU	Evolutionarily Significant Unit
FIV	feline immunodeficiency virus
FPV	feline panleukopenia virus
GC	glucocorticoid
GLMM	generalized linear mixed model
GPS	Global Positioning System
HA	hunted animals
IA	indicator animals
IPM	integral projection model
IUCN	International Union for Conservation of Nature
MCMV	murine cytomegalovirus
NIAID	National Institute of Allergy and Infectious Diseases
OIE	World Organisation for Animal Health
PAA	pre-analytical artifact
PCR	polymerase chain reaction
PVA	population viability analysis
RCV-A1	rabbit calicivirus Australia 1
RML	Rocky Mountain Laboratories
RHDV	rabbit hemorrhagic disease virus
SARS	severe acute respiratory syndrome
TTP	total testing process
TST	tuberculin skin test

Glossary

"When I use a word" Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean—neither more nor less."

Lewis Carroll, Through the Looking-Glass

In the spirit of Humpty Dumpty and Lewis Carroll, the definitions we give in this glossary are the way in which we have used the terms in this book. Many of these terms may have slightly differing definitions throughout the biological and epidemiological literature.

Terms adapted from Grenfell and Dobson (1997), Meffe and Carroll (2006), Loker and Hofkin (2015), Allaby (2005), and various internet resources.

Acaricide A chemical agent used to kill mites or ticks.

Accuracy The degree to which an individual measurement or estimate represents the true value of the attribute being measured; the proportion of all tests, both positive and negative, that are correct. (cf. **Precision**)

Adaptive management A management style in which the strategy is altered as additional information becomes available as management proceeds. Passive adaptive management uses additional information as it becomes available. Active adaptive management deliberately alters the management strategy in order to gain information to aid management.

Aetiological agent The causative agent of a disease or condition, often a microorganism or a toxin.

Aggregation Organisms show an aggregated distribution when the numbers per sampling unit (often a quadrat or, in the case of parasites, a host) are more variable than would be expected from a random (**Poisson**) distribution. The variance in counts per sampling unit will then be larger than the mean count per sampling unit. **Macroparasites** are almost invariably aggregated in their host population, the majority of hosts harboring a few or no parasites and a few hosts harboring large parasite burdens. Aggregation generally arises from some source **heterogeneity** in the host or parasite population. Clustering and overdispersion are synonymous terms. Aggregated distributions are often described by the **negative binomial distribution**.

Agroecosystem Land used for crops, pasture, and livestock; the adjacent uncultivated land that supports other vegetation and wildlife; and the associated atmosphere, the underlying soils, groundwater, and drainage networks.

Amplification host A host in which infectious agents multiply to high levels, providing an important source of infection for **vectors** or other species.

Anagenesis Evolutionary change, especially along a single, unbranched lineage.

Antibody A protein produced in the blood of vertebrates in response to an **antigen**. The antibody produced is able to bind specifically to that antigen and plays a role in its inactivation or removal by the immune system.

Antigen A substance, generally foreign, capable of inducing **antibody** formation.

Antihelminthic A drug used specifically to control helminth (i.e., parasitic worm) infections.

Arbovirus A member of a diverse group of viruses that use arthropods as **vectors** and are transmitted in their saliva to the **definitive host**.

Background extinction rate Historical rates of extinction owing to environmental causes not

influenced by human activities. Distinct and much lower than **mass extinction events**.

Barrier culling A disease elimination approach in which populations of susceptible hosts are removed from a specific region ahead of an epizootic in order to prevent entry of the disease into an area where it does not occur, or from where it has been eliminated in the past.

Basic reproductive number (basic reproduction number, basic reproductive ratio R_0) A theoretical value representing the average number of new infections that arise during the period of infectiousness of a single infectious individual who has entered a population of completely susceptible hosts. (cf. **effective reproduction number**)

Bayesian statistical methods Statistical methods derived from Thomas Bayes' theorem of conditional probability. Bayesian methods are characterized by their incorporation of prior knowledge about the quantity to be estimated, which is then modified by the observed data to generate a posterior distribution.

Binomial distribution A statistical distribution that describes the probability of observing the number of "successes" x, from a series of n independent trials in which the probability of success p remains constant. In disease ecology, if the **prevalence** of infection in a population is p, the number of infected individuals x in a sample size of n individuals is likely to follow a binomial distribution.

Biocontrol or biological control The addition of a species to an ecological community with the intention of controlling an invasive species.

Biomagnification The accumulation of toxic substances in species occupying higher trophic levels.

Bridge host A host (in most usages, other than a **vector**) that transmits infection from a **maintenance** or **reservoir host** to a **target host**. (cf. **amplification host** and **reservoir host**)

Burden of disease Mortality, morbidity, and disability in a population caused by a disease.

Bushmeat Meat from animals (usually terrestrial) that is harvested in the wild. Often a cause of wildlife endangerment and a portal for the introduction of zoonotic pathogens into human populations.

Carrier (asymptomatic) An individual infected with a parasite that may transmit infection, but which does not display symptoms of disease.

Case definition A standard set of criteria for determining whether an individual has a particular infection, disease, or syndrome. Use of an agreed-upon standard case definition ensures that every case is equivalent, regardless of when or where it occurred. Furthermore, it allows for rigorous comparison of case numbers or rate of disease, identified in one time or place against the number or rate from another time or place (Centers for Disease Control and Prevention).

Chemoprophylaxis The use of chemicals to prevent infection or disease.

Chemotherapy The treatment of infection by means of chemicals (drugs) that have a specific toxic effect on the parasite or pathogen.

Coccidia An order of parasitic protozoa.

Cohort (observational) study A particular form of longitudinal study that samples the performance of a cohort (a group of individuals who share a defining characteristic, typically those who experienced a common event, such as birth during a selected period), at various intervals throughout time. Cohort studies represent one of the fundamental designs of epidemiology and are used on "difficult to reach" answers, for instance on how risk factors affect the incidence of diseases.

Commensalism A form of interspecific association in which two species live in close association with each other, with one deriving a benefit, and the other being neither positively nor negatively affected. (cf. **Mutualism** and **Parasitism**)

Complex life cycle A life cycle in which a parasite needs to be transmitted through at least two different host species in order to complete its development. (also **Indirect life cycle**)

Confidence interval (xx%) A range of values within which the true value of a **parameter** will fall xx% of the time if a given estimation procedure is repeated a large number of times. Loosely, it is often said that there is an xx% chance that the true value of the parameter will fall within the

confidence interval. This definition is, however, closer to the **credible interval** used in **Bayesian statistics**.

Contact rate The average frequency per unit time with which susceptible individuals contact (or are sufficiently close to) infected individuals or infective stages of a parasite, such that they can potentially acquire infection.

Credible interval In **Bayesian statistics**, an interval in which an unknown parameter falls with a given probability.

Cross-sectional observation study A study that examines the infection or disease status of a host population (generally subdivided by age or sex) at a moment in time.

Definitive host see **Primary host**.

Degrees of freedom (of an estimate or test statistic) The number of independent observations used to calculate the statistic or estimate, minus the number of quantities calculated from the same dataset that were required to calculate the statistic or estimate.

Density-dependent transmission Transmission of a pathogen/parasite at a rate that is dependent (typically in a positive manner) on the population density of the host.

Digenean A parasitic helminth belonging to the platyhelminthic fluke subgroup Digenea.

Dilution effect The hypothesis that pathogen or parasite transmission to a **target host** decreases with increasing diversity of the ecological community.

Direct life cycle (or **Simple life cycle**) A life cycle in which a parasite is transmitted directly from one host to the next without an intermediate host or **vector** of another species.

Disease An abnormal condition affecting the functioning of an organism, not caused by external injury. Often used incorrectly or as shorthand to refer to a **parasite** or **pathogen** that causes disease.

Disease triangle The concept that infectious disease (both at a population and individual level) is a result of an interaction between the host, a disease-causing organism (parasite or pathogen), and the environment in which both host and pathogen occur.

Edge effect The altered biological and environmental conditions at the perimeter of a fragmented habitat; see **Habitat fragmentation**.

Effective reproduction number (R_e) The average number of secondary cases resulting from each infected individual at any point after disease has been introduced into a population, taking into account factors such as an acquired immunity or vaccination. (cf. **Basic reproduction number R_0**)

Efficacy An index of the potency of a drug or treatment, usually estimated as the average proportion of parasites in any host killed by a single dose or a short-term course of the treatment.

Eigenvalue A fundamental mathematical parameter associated with square matrices that has many important applications in population biology and epidemiology. For example, the largest (dominant) eigenvalue of a matrix describing an age-structured population represents the logarithmic growth rate of that population.

Elimination of a pathogen. Reduction to zero of the incidence of infection caused by a specific agent, in a defined geographical area, as a result of deliberate efforts. (cf. **Eradication**)

Environmental reservoir Part of the environment, either other organisms (see **Reservoir population**), or abiotic parts of the environment, in which a parasite or pathogen can be maintained in the long term, and from which it can infect a **target population**.

Enzootic transmission Relatively stable transmission of an infectious agent in an animal population.

Epizootic transmission Transmission of an infectious agent in an animal population in excess of what is normally observed in a region in a given period. The resulting wave of infection is called an *epizootic*.

Eradication of a pathogen The reduction to zero of the worldwide incidence of infection caused by a specific agent, as a result of deliberate effort. (cf. **Elimination**)

Eutrophication The overabundance of algal life (an algal bloom) in a body of water, typically as the result of human-caused nutrient (N, P) inflow. Following the eventual death of these

algae, their decomposition leads to pronounced removal of oxygen from the water column, therefore creating conditions conducive to pathogen spread.

Exotic species Species introduced to a different ecosystem than their native one, often through anthropogenic processes; such nonnative species however are not necessarily invasive.

Exposure Contact with an infectious agent required, but not sufficient for infection. Not the same as dose.

***Ex situ* preservation** Managing animals in zoos, or otherwise away from their natural habitat in order to protect them. (Contrast with ***In situ* conservation**)

Extinction cascade A series of linked extinctions whereby the extinction of one species leads to the extinction of one or more different species.

Extinction vortex A set of self-reinforcing internal processes (such as inbreeding depression or demographic stochasticity) that can lead to the eventual extinction of small populations even in the absence of external stressors. The tendency of small populations to become progressively smaller in each generation, eventually going extinct.

Extinction rate (background) "Normal" low-level rates of extinction owing to background environmental causes, not influenced by human activities or other catastrophic events (see **Mass extinction event**).

Fitness The extent to which an organism is adapted to its environment, measured by the number of viable offspring it leaves behind relative to other individuals in the population.

Focal culling ("reactive culling," "point infection control") An approach used to eliminate disease in animals. The entire group on an "infected" farm or a herd is euthanized, and culling may extend to adjacent premises, to remove potential sources of infection and reduce availability of susceptible animals. The technique requires rapid identification of cases, prompt intervention, and restriction of movement of animals into and out of the cull site and is best used in situations where good access exists to the animal population.

Fomite An inanimate object or substance that transfers a pathogen from one host to another.

Force of infection For **microparasites**, the rate (per unit of time) at which susceptible individuals in a given population acquire infection. For **macroparasites**, the rate at which hosts acquire additional parasites.

Frequency-dependent transmission A term used to describe disease transmission that does *not* depend on the density of infected and susceptible hosts but instead on the frequency with which a transmitting event occurs. Spread of vector-transmitted pathogens and sexually transmitted diseases is often frequency dependent.

Genetic drift Genetic changes and losses that occur by chance, especially evident in small populations.

Glochidium/ia The larval stage typical of many types of freshwater bivalves (mussels) that attaches to the gill filaments of fish where it lives as an ectoparasite. Ultimately it drops off and settles on the bottom of the water body to continue its development into an adult mussel.

Habitat The physical environment in which a species is found.

Habitat corridors Strips of land, typically covered by natural vegetation, which connect patches of natural habitat.

Habitat fragmentation The process by which a large, continuous area of habitat is both reduced in area and divided into two or more sections (fragments).

Helminth A member of one the five classes of parasitic worms: monogeneans, digeneans, cestodes, nematodes, and acanthocephalans.

Herd immunity Reached when a sufficiently high proportion of a population is immune (either as a result of vaccination or acquired immunity) that the prevalence of infection no longer increases in the population.

Herd immunity threshold The minimum level of herd immunity that prevents sustained transmission of an infectious agent in a population. Depends on characteristics of the infectious agent, the host population, and the environmental conditions.

Heteroxenous A parasitic organism that utilizes more than one host during its life cycle.

Hematozoan A parasitic organism residing primarily in the blood of the host.

Host Any animal or plant that under natural conditions provides sustenance or shelter to a parasitic organism.

Horizontal transmission The most common type of pathogen/parasite **transmission**, in which an infected individual infects another susceptible individual of the same species.

Hypothesis testing A statistical approach in which a **null hypothesis** continues to be accepted following an experiment, unless the data collected indicate that the null hypothesis is sufficiently unlikely to be true. In that case an alternative hypothesis is accepted.

Immunity the ability to combat **infection** or **disease** owing to the presence of **antibodies** or activated cells. Typically divided into three types: **acquired immunity** is conferred on an individual following recovery from a disease; **natural** or **innate immunity** is inherited from parents, or in some cases antibodies may be passed across the placenta and therefore are present in the blood at birth; and **artificial immunity** may be induced by the injection of a vaccine or antiserum and confers protection of variable duration to a pathogen.

Immunosuppression Suppression of the immune response by drugs, parasites, or the host's own immune regulatory mechanisms.

Inbreeding The mating of individuals who are more closely related than by chance alone.

Inbreeding depression Lowered reproductive rates, or production of offspring with lowered survival and reproduction, following mating among close relatives or self-fertilization.

Incidence rate The ratio of the number of new events (e.g., infections) during a defined time period to the population at risk of experiencing the event.

Incubation period The time interval between the acquisition of infection and the onset of clinical signs. (cf. **latent period** and **serial interval**)

Indirect Life cycle (or **Complex life cycle**) A life cycle that requires one or more **intermediate hosts**, or **vectors** before the **definitive host** is reinfected.

Infection The colonization and replication of a parasitic organism that gains sustenance or shelter from the body of a host, whether or not that host experiences ill health.

Infectious (or contagious) disease Disease caused by infection with a parasite that can be transmitted from one individual to another either directly or, indirectly, through a **vector**.

***In situ* conservation** Managing species in their natural environment. (cf. ***Ex situ* conservation**)

Intensity of infection Used inconsistently in the literature: either the mean number of parasites within infected members of the host population or the mean parasite burden of the entire population. Unless **prevalence** is 100%, the latter will be smaller than the former.

Intermediate host (also **secondary host**) A host required for a parasite's life cycle, but not the host inside which parasite sexual reproduction occurs.

Invasive species A species occurring and expanding its distribution outside its natural range, typically introduced directly or indirectly by to human activities (see **exotic species**).

Keystone species Select species that have a disproportionate effect on the organization of a biological community and the loss of which may have far-reaching consequences for community structure.

Koch's postulates A set of four criteria used to determine whether a causative relationship exists between a microorganism and a disease. First expressed formally by the German physician Robert Koch in the nineteenth century.

Latent infection An **infection** that is causing no disease.

Latent period Interval between acquisition of infection by a host and its ability to transmit infection. (cf. **Incubation period** and **Serial interval**)

Likelihood In statistics, the probability of observing values of one or more model parameters, given a particular set of data. The set of parameters at which the likelihood is maximized are called the **maximum likelihood estimates**.

Macroparasites Parasites that in general do not multiply within their definitive hosts but instead produce transmission states (eggs and larvae) that pass into the external environment or to vectors (e.g., the parasitic helminths and arthropods). Typically multicellular and visible with the naked eye.

Maintenance host A host species, in which a parasite or pathogen can be maintained indefinitely and from which infection can be transmitted to another **target** species. See **Reservoir population**, which is a slightly more general term.

Mass extinction event The terminal extinction of a very large number of taxa that occurs over a relatively short geologic time. Mass extinction events are thought to be caused by catastrophic insults of global reach such as disruptions of the planetary biogeochemical cycles following extensive volcanic eruptions or asteroid impacts. Five major mass extinctions have been identified in the fossil record, one each at the end of the Ordovician, Devonian, Permian, Triassic, and Cretaceous geologic periods. Earth is presently at the beginning of a sixth mass extinction triggered by human activities.

Maximum likelihood estimates For a given statistical model and set of data, the parameter estimates at which the **likelihood** is maximized.

Microparasites Parasites that undergo direct multiplication within their definitive hosts. Microparasites are characterized by small size, short generation time, and a tendency to induce immunity to reinfection in those hosts that survive the primary infection. Duration of infection is usually short in relation to the expected life span of the host.

Microparasitism Infection with a microparasite.

Metapopulation A shifting mosaic of frequently transient populations, linked by some degree of migration; a population of populations.

Morbidity Any departure, subjective or objective, from a state of physiological or psychological well-being.

Mortality rate The rate per unit time at which individuals die; or alternatively the ratio of the number of deaths during a defined time period to the number of hosts at risk of dying during that period.

Mutualism A form of interspecific association in which two species live in close association with each other, with both deriving a benefit. (cf. **Commensalism** and **Parasitism**)

Negative binomial distribution A discrete probability distribution for counts, giving the probability that a sampling unit has x items in it, in situations where items are **aggregated**. A key property of the negative binomial distribution is that the variance in the number of items per sampling unit is greater than the mean number of items per sampling unit. Negative binomial distributions are described by two **parameters**: the mean, and a parameter usually denoted k, which describes the degree of aggregation. Small values of k represent highly aggregated distributions, and as k approaches infinity, the negative binomial distribution approaches a **Poisson** distribution. Distributions of parasites among hosts are often well described by negative binomial distributions.

Nidus Specific location of a given disease; the result of a unique combination of ecological factors that favors the maintenance and transmission of the disease organism.

Nonselective culling, area-wide ("proactive culling," "host population reduction") A disease management approach that aims to stop the spread of a density-dependently transmitted pathogen by reducing wildlife host population densities through indiscriminate culling. See **Selective culling**.

Null hypothesis In hypothesis testing, what will continue to be believed in the absence of sufficient evidence to the contrary. Usually, it is that "nothing is going on": in an experiment it might be that the response does not differ depending on whether experimental subjects are exposed to a treatment or a control.

Ontogenetic Pertaining to the development of an individual from fertilization of an egg to adulthood and death.

Oocyst The intermediate stage in the Apicomplexan life cycle following the union of the micro- and macrogametocyte in which sporozoites are produced.

Parameter A constant number that forms part of the specification of a mathematical model

(e.g., the transmission rate of a pathogen, or the variance in a normal distribution). Parameters are usually theoretical, unknown quantities that need to be estimated from data, frequently derived from a sample taken from a wider population.

Parasite An organism exhibiting a varying but obligatory dependence on another organism, its **host**; typically detrimental to the survival and/or **fecundity** of the host.

Parasitemia The presence of a parasite in the blood of the host.

Parasitism A form of interspecific association in which two species live in close association with each other, with one (the **parasite**) living in or on the other and deriving a benefit, and the other (the **host**) being negatively affected. (cf. **Mutualism** and **Commensalism**)

Pathogen A parasitic organism, typically unicellular or a virus (hence also a **microparasite**), that causes disease or morbidity in its host.

Pathogenicity The degree to which a parasite tends to cause disease in its host, and the severity of the disease caused.

Poisson distribution A discrete probability distribution for counts, giving the probability that a sampling unit has x items in it, given that the overall mean number of items per unit is known. It applies if items are distributed independently between sampling units. A key property of the Poisson distribution is that the variance in the number of items per sampling unit is equal to the mean number of items per sampling unit. In the context of parasite distributions among hosts, the number of parasites per host would follow a Poisson distribution if the fact that a host has acquired one parasite provides no information on whether it is more or less likely to acquire another parasite, compared with other members of the host population. This is not a common situation: parasites are usually **aggregated** in their distribution among hosts and the distribution is often better described by a **negative binomial distribution**.

Power Statistical power in a hypothesis test is the probability that the **null hypothesis** will be rejected in favor of the **alternative hypothesis**, given that the alternative hypothesis is true. Therefore, the higher the power, the more likely the test can detect a true effect. A variety of factors affect the power of a test including the sample size, the effect size, and the inherent variability in the data.

Power analysis An analysis used to determine the minimum necessary sample size so that a test or experiment can detect an effect at the desired level of significance.

Precision The closeness to each other of repeated measurements or estimates of the same quantity. (cf. **Accuracy**)

Prepatent period The time from infection (generally first infection) until the host shows symptoms (synonymous with **incubation period**).

Prevalence (or **Prevalence Rate**) The proportion of the host population with infection or disease, often expressed as a percentage. A measure of how widespread an infection or disease is.

Primary host The host in which a parasite's sexual reproduction normally occurs (also termed **definitive host**).

Random sample A sample is a subset of the population and in statistics it is used to provide information about the whole population. As a result, it needs to be an unbiased representation of the entire population. Drawing a random sample is a common method for achieving this unbiased representation. In a simple random sample, each member of the population has an equal probability of being included in the sample. The number of units in the sample is called the sample size, often denoted n.

Recrudescence Reappearance of disease in a host whose infection has been quiescent (i.e., without symptoms).

Reintroduction An attempt to establish a species in an area that was once part of its historical range, but from which it was been extirpated. Reintroduction is prime occasion during which attendant parasites/pathogens may also get accidentally introduced. (cf. **translocation**)

Replicate A random subset of the entire available sample (i.e., sampling pool) that has been drawn for a particular survey. Sample replicates help measure variation in an experiment, so that any differences between treatment groups can be better evaluated.

Representativeness In a population, the extent to which a selected sample represents the overall population in terms of specific biological characteristics; in a reserve system, the quality of a set of sites that together include all or most existing biodiversity elements.

Reservoir population A host population, or group of populations, in which a parasite or pathogen can be maintained indefinitely and from which infection can be transmitted to another **target population**. Reservoirs are often (but not necessarily) different species from the target population and will frequently be more **tolerant** of infection than the target population. See **maintenance host**.

Resistance (as applied to parasites) The reduction in susceptibility to chemotherapy or to chemical vector control.

Resistance (as applied to hosts) The ability to limit parasite burden if exposed to infection. One host is more resistant than another if it develops a lower parasite burden when exposed to the same infective dose. (cf. **Tolerance**)

Response variable The variable that investigators are trying to explain or predict and typically the focus of a question in a study. Also known as the dependent or outcome variable, its value is predicted, or its variation is explained by explanatory (independent) variable(s). In an experimental study, it is the outcome that is measured following manipulation of the explanatory variable(s).

Risk assessment The process of identifying, evaluating, and managing the risks that may arise from a given action or activity.

Sample A group of individuals or items that are selected from a larger population for measurement. The sample should be representative of the population to ensure that one can generalize the findings from the sample to the population as a whole.

Sampling frame A sampling frame is a list or other device used to define a researcher's population of interest. Hence a sampling frame defines a set of elements from which a researcher can select a sample of the target population.

Saprophytic (or **saprotroph**) An organism that absorbs soluble organic nutrients from inanimate sources (e.g., dead plant or animal matter or dung).

Secondary host See **Intermediate host**.

Selective culling ("test-and-cull") A disease eradication approach in which animals are tested for infection, and those that test positive are killed to prevent further disease transmission. It is the least controversial form of culling, because only infected individuals are removed; however it is also challenging because it requires both the identification of infected individuals under field conditions, and the ability to test a substantial proportion of the population. See **Nonselective culling**.

Sensitivity analysis A method used to determine the robustness of an assessment by investigating the degree to which the results and conclusions of the assessment are shaped by the methods, models, or assumptions that went into the analysis. It often involves modifying these methods/models/assumptions and then determining to what extent the results change.

Serial interval The time between the acquisition of infection by a host and transmission onto another host. The serial interval is usually longer than the **latent period** because onward transmission does not necessarily occur as soon as a host becomes infectious.

Significance level A measure of the strength of the evidence that must be present in a sample before one rejects the **null hypothesis** (of no difference) and accepts the **alternative hypothesis** that an effect is statistically significant. In classical **hypothesis testing**, the researcher selects the significance level before conducting the experiment. Typically denoted as alpha or α, it is the probability of rejecting the null hypothesis when it is true (making a **Type I error**). For example, a significance level of 0.05 indicates a 5% risk of concluding that a difference exists when there is no actual difference.

Simple life cycle See **Direct life cycle**.

Species–area relationship The positive relationship between the size of natural areas and the number of species there. One of the fundamental patterns in ecology.

Stochastic Random; a random process.

Stratified random sampling A method of sampling that involves the division of a population into smaller subgroups known as **strata**. In stratified random sampling, or stratification, the strata are formed based on individuals' common characteristics such as sex or age. Within each stratum individuals are then selected randomly.

Stratum In statistics, a stratum (plural strata) refers to a subset of the population that is being sampled. Stratification therefore consists of dividing the population into strata within each of which an independent sample can be chosen. Stratification may be conducted based on geographical criteria, e.g., by dividing up the sampled area into subareas; or by referring to some other quality of an individual, e.g., by dividing the individuals into strata according to sex. It ensures that all subsets of a population are equally sampled.

Superspreaders A small proportion of the infected members of a population that transmit the parasite or pathogen at a rate substantially higher than most infected members of the population.

Susceptibility Accessible to, or liable to infection by a particular parasite.

Susceptible individual An individual that can get infected by a pathogen either because it has never developed immunity (i.e., it is immunologically naive) or because it has lost past immunity.

Synergism An interaction in the way two factors affect another variable. This may be either positive or negative (in which case the final effect is bigger/smaller than the sum of the individual factor effects).

Systematic samples Samples collected using a systematic sampling format. In this format, an investigator chooses individuals from a target population by choosing a random starting point and then selecting sample members after a fixed "sampling interval," e.g., every 10th individual. If the population order is random or random-like (e.g., alphabetical), then this method will provide a representative sample that can be used to draw conclusions about the population. Systematic sampling is popular because it is simpler and more straightforward than random sampling and more conducive to covering a large area.

Target host species or population A host species or population of particular interest in a given situation. In the context of conservation biology, the target population will often be an endangered species or a species highly susceptible to the parasite.

Test accuracy This refers to the ability of a test to differentiate between the patient (infected) and healthy cases correctly. To estimate the accuracy of a test, one needs to calculate the proportion of true positive and true negative in all evaluated cases.

Test reliability This refers to how dependably or consistently a test can measure a characteristic. This consistency of a measure relates to whether the test results can be reproduced repeatedly under the same conditions.

Test sensitivity Sensitivity and specificity are measures of a test's ability to correctly classify an individual as having a disease or not having a disease. Sensitivity refers to a test's ability to designate an individual with disease as positive. A highly sensitive test means that there are few false negative results, and thus fewer cases of disease are missed. It is desirable to have a test that is both highly sensitive and highly specific. This is frequently not possible, and typically there exists a trade-off. In many clinical tests, there are some individuals who are clearly normal, some clearly abnormal, and some that fall into the gray area between the two. As a result, careful choices must be made in establishing test criteria for positive and negative results (see **Test specificity**).

Test specificity Specificity and sensitivity are measures of a test's ability to correctly classify an individual as having a disease or not having a disease. The specificity of a test is its ability to designate an individual who does not have a disease as negative. A highly specific test means that there are few false positive results. It may not be feasible to use a test with low specificity for screening, since many individuals without the disease will screen positive, and potentially receive unnecessary diagnostic procedures (see **Test sensitivity**).

Test validity This is the extent to which a screening test accurately identifies diseased and

nondiseased individuals. A test that has high validity produces results that correspond to the "real" infection status of an individual, as determined by some "gold standard" test.

Tolerance The ability to limit the harm caused by a given parasite burden. One host is more tolerant of infection than another if, given the same parasite burden, its fitness is higher. (cf. **Resistance**)

Translocation A management technique often used in mitigation for endangered species protection whereby an individual, population, or species is removed from its habitat to be established in another area of similar or identical habitat. An occasion during which attendant parasites/pathogens may also get accidentally introduced.

Transmission The process by which a **parasite** passes from a source of **infection** to a new **host**. Multiple types occur including **horizontal**, **vertical**, sexual, trophic, vector-borne, waterborne etc., with the first two being the most common.

Trematode Any of the parasitic flatworms of the class Trematoda; characterized by a thick outer cuticle and one or more suckers to attach to the host.

Trophic transmission A mode of transmission of an infectious agent that depends on the consumption of the one host by another.

t-statistic In statistics, the t-statistic is the difference between the estimated value of a parameter and a hypothesized value (which is often zero), divided by the standard error of the estimate. It is often used to test whether there is evidence that two means differ. Another common use is to test the hypothesis that the estimated value of a parameter differs significantly from zero.

Two-tailed In statistics, a two-tailed test is a method in which the critical area of a distribution is two-sided, and tests whether a sample is greater than, or less than, a certain range of values. It is used in null hypothesis testing and testing for statistical significance. If the sample being tested falls into either of the lateral critical areas, the alternative hypothesis is accepted instead of the null hypothesis. A test of a statistical hypothesis, where the region of rejection is on both sides of the sampling distribution, is called a two-tailed test.

Type I error In a hypothesis test, a type I error occurs when a null hypothesis that is actually correct is rejected. The probability of committing a type I error equals the **significance level** one sets for the hypothesis test. For example, a significance level of 0.05 indicates that one is willing to accept a 5% chance of wrongly rejecting the null hypothesis. For a given set of data and statistical test, decreasing the probability of making a type I error increases the probability of making a **Type II error**.

Type II error In a hypothesis test, a type II error occurs when one fails to reject a null hypothesis that is actually false. In other words, one obtains a nonsignificant test result even though a true population effect actually exists. Some combination of a small sample size, inherent variability in the data, and bad luck with random sample error might have obscured the population effect. One can decrease the probability of a type II error by increasing the **power** of the test.

Vector An organism that carries and transmits a pathogen between hosts. Vectors are typically small-bodied and mobile and are often insects or other invertebrates.

Vector-borne transmission A mode of transmission of an infectious agent that depends on infection of a relatively small-bodied mobile host (termed **vector**), typically an invertebrate such as an insect or a tick.

Vertical transmission A mode of transmission in which an infectious agent passes from a parent host to its offspring.

Virulence Broadly defined the ability of a pathogen to cause damage to the host.

Zoogeography The study of the geographic distribution of animals at different taxonomic levels.

Zoonosis Infectious disease of humans caused by an infectious agent that normally circulates among nonhuman animal **reservoirs**.

Introduction

As we write this, the raging COVID-19 pandemic is reminding humanity of a lesson many of us had forgotten over the past century of rapid medical advances: the power of infectious disease to affect not just our health and well-being, but to drastically reshape the world around us. At the same time, this pandemic is also a reminder of the critical role of the environment, including ecological species interactions, in shaping disease outbreaks. While the circumstances of the origin of SARS-Cov-2 will undoubtedly become clearer in the future, its animal origins are undeniable, thus underscoring the role of free-ranging wildlife as a perennial source of new and emerging pathogens.

An extensive body of research over the past 20 years has documented the origins and processes of pathogen emergence, and has also offered important avenues for infectious disease control and prevention. The same research has also revealed that infectious diseases pose a significant danger not just for humans but also for many wildlife species. Indeed, emerging infectious diseases are increasingly recognized as one of the major forces driving species extinction. The same anthropogenic processes that have led to increasing emergence of zoonotic diseases affecting humans, namely habitat modification and destruction, climate change, and increased global connectivity, also have led to increasing emergence of wildlife disease. Addressing the challenges that wildlife faces from new pathogens is particularly difficult for numerous reasons, and no work currently exists that synthetically integrates recent advances in the field. With this book, we aim to fill this gap and help elucidate the role of emerging disease ecology in conservation.

To paraphrase our colleague Bart Kempenaers, books differ from scientific papers because they not only state and establish facts, they also establish arguments, synthesize fields, and propose new directions—in so doing, they have the ability to change perspectives and minds. To that extent, the purpose of this book is threefold: first and foremost, to make the argument that parasites and pathogens play a critical role in species conservation and need to be considered throughout any conservation management effort; second, to serve as a gentle academic introduction to wildlife infectious disease ecology for people not directly involved in the field; and last, to serve as a practical "how-to" guide for setting up a study of pathogenic organisms in natural populations.

Overall, this book is intended to stimulate interest and summarize the current state of the field. It is also our hope that it can serve as an introduction to the often-overwhelming literature for people who are not experts in this rapidly expanding and particularly interdisciplinary field.

Intended audience

This book, focusing largely on the topic of disease ecology, sits thematically at the nexus of at least three more established disciplines: wildlife veterinary science, conservation biology, and theoretical population ecology. Because each of these fields comes with its own priorities, values, biases, and its own specific vocabulary, one of the early challenges while writing the book was to integrate these distinct approaches and to produce a text that would be accessible to readers from each field.

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The intended audience of this book includes students and practitioners from each of these fields. We hope that it can act as a bridge that will allow members of different disciplines to become familiar with basic concepts in disease ecology and conservation. More specifically, this book is aimed at advanced students, practicing conservation biologists, and anyone interested in the study of wildlife diseases in nature. To ensure accessibility of the content, we have tried to limit the amount of information to the most pertinent works and to enrich the book with numerous figures and images. References to technical literature are restricted to the most important works, and each chapter is accompanied by its own reference section to ensure its standalone relevance. Furthermore, we have tried to use approachable language and have included an extensive glossary that handles the more technical terms and concepts discussed in the book.

Background and focal systems

As already pointed out by others before us, the study of infectious diseases has been one of the triumphs of modern ecology. The past 20 years have seen a blossoming of the field of disease ecology with numerous key studies advancing our understanding, not just of the role of parasites and pathogens in natural ecosystems but also of the associated ecological and evolutionary host–pathogen dynamics. At this point, significant progress has been made and it is an excellent time to summarize the present state of the field.

We have intentionally focused this book on terrestrial vertebrate organisms. While occasional examples involving marine, invertebrate, and even plant species, are included, we have limited ourselves to terrestrial vertebrates for two major reasons: first, host–parasite interactions are much better understood in terrestrial vertebrates than in other groups of hosts; and second, whether one agrees with this or not, they are the most common focus of conservation management and restoration projects.

Within this group, we return repeatedly to three study systems that are, by virtue of the known detail and our personal research background, disproportionally important. We have chosen these because they are particularly prominent in the conservation literature and because they illustrate different aspects of managing infectious diseases of conservation significance. Further, by returning to the same case studies repeatedly, we show how a range of approaches can be applied to solve these difficult problems. More specifically:

Avian malaria and bird pox have devastated the Hawaiian avifauna following the introduction of the mosquito vector *Culex pipiens* in the mid-nineteenth century. Several dozen species of endemic birds have become extinct and several others have contracted in distribution largely because of these diseases. Owing to the disproportionate conservation impact and available funding, extensive research has already been conducted on this system. As a result, we have a comparatively good understanding of the transmission dynamics of these pathogens, their impact on the native bird populations, as well as possible management approaches. Avian malaria and bird pox are important examples of the class of vector-borne pathogens, and this system also illustrates multiple disease-related issues associated with anthropogenic climate change. This case study is first introduced in Chapter 1 and then also referred to in Chapters 2, 3, 6, 7, 12, and 14.

Chytridiomycosis is an emerging fungal disease that has had the greatest biodiversity impact of any known vertebrate pathogen. First identified in 1998, *Batrachochytrium dendrobatidis*, the causative agent of the disease, is directly responsible for over 100 global frog species extinctions, particularly in Latin America and Australia. In addition, this pathogen has precipitated broad-scale population declines on every continent where frogs can be found. More recently, *Batrachochytrium salamandrivorans*, a related pathogen, has also led to mass mortalities of newts and salamanders in Europe. The origin of both waterborne fungi appears to be in Asia, and they have been disseminated worldwide owing to human activities. Supported in each area by a few host species that are relatively tolerant of infection and can act as reservoirs of infection, these pathogens have been transmitted to other highly susceptible species, which can then be driven to extinction. Chytridiomycosis holds important lessons for conservation biologists as an

example of the threats posed by persistent, multi-host pathogens. Chytridiomycosis is introduced in Chapter 1 and discussed in Chapters 2, 3, 7, 9, 10, 11, 12, and 14.

Tasmanian devil facial tumor disease (DFTD) is a transmissible cancer, first detected in 1996, which threatens to cause the extinction of the largest marsupial carnivore still surviving. Tumor cells are transmitted between Tasmanian devils by biting during competitive or mating interactions. These tumors are clonal descendants of a single tumor that arose in a nerve cell of a female devil, which must now be long dead. More recently, a second transmissible tumor has appeared in Tasmanian devils, with a male origin. The spread of this cancer has been facilitated by the underlying severe loss of genetic diversity in Tasmanian devil populations. While this is a highly unusual pathogen, it is one of the very few cases in which a novel infectious disease has been extensively researched from its first emergence, so that insights can be gained into its impact and spread throughout almost the entire geographic range of a species. This case study also illustrates the power of the diverse approaches that have been applied to understand the disease and manage its impact on the host population. DFTD is introduced in Chapter 1, and is further discussed in Chapters 9, 10, 11, 14, and 16.

Beyond these key study systems, we have gone to great pains to expand coverage of the pathogens discussed. We have tried to include information from disease and conservation from diverse parts of the world, especially from less developed countries that harbor important biological diversity and underappreciated ecological systems.

Book structure

The book is structured around three sections. First, there are three general overview chapters, starting with an introduction of the general principles of conservation biology for non-conservationists, some principles of infectious disease ecology in natural ecosystems for conservation biologists, and, drawing the two strands together, a chapter on interactions between human activities and wildlife disease. Second, a series of methodology chapters follows, discussing principles of planning and experimental design for wildlife disease studies, techniques for animal capture and data acquisition, methods for detecting disease agents in the field and laboratory, and development of mathematical models together with their parameterization. The final section of the book deals with combining the theory and methodology to manage emerging disease threats. Following an introductory chapter on planning management strategies, we discuss preventing infectious disease arriving in an ecological community, eliminating disease once it has arrived, and ensuring that populations persist if disease cannot be successfully eliminated. The next chapter considers an entirely different application of management of infectious disease in a conservation context, which is to use a parasite or pathogen to control a pest species. The final chapter considers the ethical and societal issues that may arise when managing infectious diseases in wildlife populations.

In summary, this book combines an introduction to basic principles of wildlife epidemiology with practical veterinary approaches and theoretical ecology insights. It is not a detailed mathematical treatise of theoretical wildlife disease ecology, nor a comprehensive review of veterinary field methods. Readers interested in this should consider the specialized literature available from other authors cited throughout the book.

Disease ecology has expanded so rapidly in the past several decades that it is no longer possible to include all relevant references in this work. One of the hardest choices has been to decide which works to cite in this book. We apologize to our colleagues who may not find their work cited—any such omissions are not intentional.

We tried to ensure the book is as accurate and free of errors as possible. Nevertheless, this highly interdisciplinary subject has become sufficiently complex and broad that it is easy for mistakes and omissions to occur. Any mistakes are ours alone.

We hope that this book will raise awareness of the dangers presented of infectious organisms for threatened biodiversity and encourage further study of this fascinating and rewarding field.

JF, Ann Arbor
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PART I

Epidemiological Background