Of Mice and Schoolchildren: A Conceptual History of Herd Immunity

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See also Jones, p. 1376.

This article explores a tension at the core of the concept of herd immunity that has been overlooked in public and scientific discussions—namely: how can immunity, a phenomenon of individual biological defenses, be made relevant to populations? How can collectives be considered "immune"? Over the course of more than a century of use of the term, scientists have developed many different understandings of the concept in response to this inherent tension. Originating among veterinary scientists in the United States in the late 19th century, the concept was adopted by British scientists researching human infectious disease by the early 1920s. It soon became a staple concept for epidemiologists interested in disease ecology, helping to articulate the population dynamics of diseases such as diphtheria and influenza. Finally, though more traditional understandings of the concept remained in scientific use, in the era after World War II, it increasingly came to signal the objective and outcome of mass vaccination. Recognizing the complexity of scientific efforts to resolve the paradox of herd immunity may help us consider the best distribution of immunity against severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2). (*Am J Public Health*. 2021;111(8):1473–1480. https://doi.org/10.2105/AJPH.2021.306264)

During the COVID-19 pandemic, no scientific term has been the subject of more dispute than "herd immunity." Debate over the concept has taken the appearance of a disagreement over the scientific viability and ethics of achieving herd immunity via infection.[1] This appearance, however, has obscured a deeper intellectual tension at the heart of the concept: how can immunity, a condition constituted in the biological defenses of the individual, be attained by a population? How can collectives be thought to have become "immune"? While scientists and historians have long discussed the centrality of the analytic of self-other in immunology,[2] herd immunity points to the ongoing problem of articulating the immunological defenses of collectives. Some recent examples make clear that different solutions to this core conundrum are resulting in the term being used to denote very different phenomena during the ongoing pandemic.

Invoking a relatively recent understanding as it pertains to disease elimination via vaccination, one virologist recently wrote that herd immunity has "never been achieved through naturally acquired infections and is only possible at global population scale through mass immunization."[3] Yet, drawing on an older but equally widespread understanding of the concept as the point at which an epidemic subsides and a new pathogen becomes endemic, another virologist suggested that 10 previous influenza pandemics, including that of 1918–1919, ended "most likely, by a herd immunity mechanism, when at least 30% of the population had been infected."[4] To add further confusion, the term is sometimes deployed in a nonspecific sense, with one prominent British scientist recently stating that London has "quite a lot of herd immunity."[5] These few examples demonstrate some of the ways scientists have conceptualized immunity as an attribute of populations. This article suggests that the long history, beginning in the late 19th century, of scientific efforts to think of populations as immune may offer insight into the relevance of the concept to the ongoing pandemic.

EARLY RUMINATORS

The earliest use of the concept uncovered by an extensive literature review was in 1894 by America's first doctor of

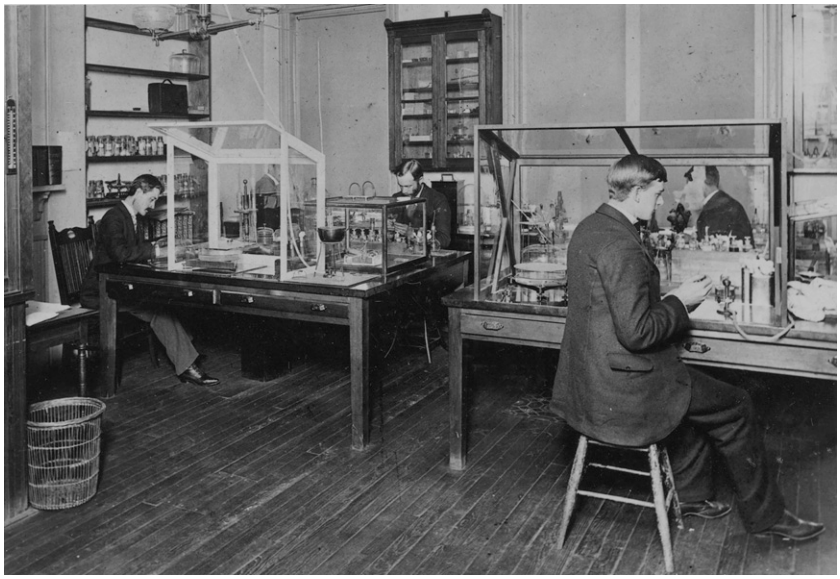

FIGURE 1— Inside the Laboratory for Animal Pathology at the Bureau of Animal Industry, 1894, Washington DC.

Note. Depicted from left to right: medical illustrator W. S. D. Haines and bacteriologists and pathologists C. F. Dawson, R. Stewart, and Veranus Alva Moore.
Source. Courtesy of Special Collections, USDA National Agriculture Library (https://www.nal.usda.gov/exhibits/speccoll/items/show/8226). Published with permission.

veterinary medicine and the first director of the US Department of Agriculture's Bureau of Animal Industry, Daniel Elmer Salmon. In that year, Salmon, after whose research *Salmonella* was later eponymously dubbed,[6] used the term in a report on animal nutrition given to the American Veterinary Medical Association. Salmon reported that, in addition to the selective breeding of animals, their "hardiness and vigor . . . may be aided by intelligent care and by scientific feeding." He frowned upon the "exclusive feeding of corn so largely practiced in hog-raising," which led to the "abnormal development of the animal body" and weakened its "powers of resistance and predisposes to disease." Experience of disease outbreaks in swine fed a poor diet and those fed a more nutritious diet demonstrated that the former were far likelier to succumb to disease. "These facts show something besides individual immunity," Salmon reported. "They demonstrate the possibility of obtaining herd immunity." Though there remained "much still to learn about this subject," he believed that "with hygienic surroundings, proper exercise, proper food, and by practicing the principles of breeding already enumerated," farmers could develop "animals with more than ordinary power of resisting both sporadic and epizootic diseases."[7] In what appears to be the earliest published use of the term, "herd immunity" indicated the "powers of resistance" against disease in general attained through good breeding, sanitary conditions, and scientific nutrition.

Salmon's understanding of immunity was very different from that held by scientists today, a fact he articulated in 1886 when he criticized none other than Louis Pasteur. Scorning the Frenchman's extrapolations from the laboratory to life in the field, Salmon insisted that the "body is very different from a culture flask to which nothing gains entrance and from which nothing is eliminated. . . . Immunity is probably never absolute, but simply relative" and because of the "vital resistance" of cellular life, even "the tissues of the most susceptible individuals are not suited to the growth of microbes when the functions of the cells are normally performed." Problems for the organism arose when "the resistance of the tissues is in some way overcome, the microbes multiply and the disease is produced."[8] His subsequent description of the concept of herd immunity reflected his understanding of immunity as the vital resistance of cellular life to agents of disease, a vitality that could be cultivated by proper scientific management.

Further reference to herd immunity does not seem to appear in publications for another 20 years. However, the fact that later reference to the term came from within the same bureau of which Salmon had been director suggests it was probably used privately within the organization across this period. In a recent history, Jones and Helmreich discussed use of the term by two veterinarians in the bureau beginning in 1916. Researching brucellosis among cattle, a disease also known as "contagious abortion" because of the miscarriage it caused, scientists George Potter and Adolf Eichhorn suggested overturning the practice of destroying infected heifers in favor of isolation until they had recovered and could be reintroduced into the herd.[9] Experiments suggested that cattle recovered from the disease usually developed immunity to future disease. As a degree of immunity seemed to be passed on to future calves, the pair suggested that "a herd immunity seems to have developed as the result both of keeping the aborting cows and raising the calves."[10]

While Potter and Eichhorn evidently thought of immunity to brucellosis as a

more specific quality than Salmon's "powers of resistance," their understanding of the concept did not appear to be limited to inherited, partial immunity. They often emphasized the role of breeding and sanitation and wrote of resistance as more than immunity. In 1920, Potter insisted that "the mode of living" of the range cow gave it "greater resistance to ward off the effects of the disease" than the dairy cow, the latter living in a less salubrious environment and "subjected to the weakening influence of the artificially stimulated function of milk production." Resistance was more expansive than acquired or inherited immunity, and farmers were encouraged "to build up herd immunity through the selection of prolific, resistant and immune cows and their offspring."[11] Nurturing immune herds entailed more than simply raising the calves of heifers recovered from the disease.

THE ECOLOGY OF HERD IMMUNITY

As other historians have noted, the first to use the term with a bearing upon human infectious diseases were British bacteriologists William Whiteman Carlton Topley and Graham Selby Wilson.[12] Crucial to their understanding of the concept was its irreducibility to the sum of individual immunities within a population. In 1923, they described findings from experimental epidemics they had conducted on caged mice populations. Unsurprisingly, these experiments showed "a decreasing mortality with an increasing proportion of immunized mice." However, the pair insisted that immunity in collectives was not merely the sum of the number of immune individuals and that "the question of immunity as an attribute of a herd should be studied as a separate problem, closely related to, but in many ways distinct from, the problem of the immunity of an individual host."[13] As historian Olga Amsterdamska clarified, Topley approached epidemics "as events affecting collectives rather than individuals" and insisted that they "could not be reduced to individual cases of disease."[14]

For Topley and Wilson, herd immunity described an uneven, nondetermined formation of resistance across a population operating to restrict disease transmission. The notion of resistance captured a gradation of immunity to infection and disease. Within any given population, individuals did not fall into the simple binary of immune or susceptible but were positioned along a continuum of resistance itself conditioned by the distribution of resistance in the surrounding population. As Topley explained in 1935: "With herds, as with individuals, there are, of course, all gradations between complete immunity and complete susceptibility."[15] The resistance of the individual was intimately enmeshed in the resistance of its "herd," and the resistance of that herd was greater than the sum of its parts. The pair clarified the implications of this insight for public health when they asked:

> Assuming a given total quantity of resistance against a specific bacterial parasite to be available among a considerable population, in what way should that resistance be distributed among the individuals at risk, so as best to ensure against the epidemic spread of the disease, of which the parasite is the causal agent?[16]

In later years, they understood the spread of disease to be conditioned by a population's "herd structure," which included its "spatial relationships," "as well as all those environmental factors that favor or inhibit the spread of infection from host to host."[17] Attempting to capture the nature of immunity at the population level, Topley and Wilson deployed the concept of herd immunity to understand how populations might best prevent the spread of disease. This interpretation arose from the unfortunate fact that, for most diseases, there were no vaccines, forcing public health strategists to consider the most effective use of natural immunity.

Precisely how and when the term crossed from American veterinary science to British bacteriology and epidemiology remains unclear. Epidemiologist Paul Fine claimed that Wilson told him in 1981 he first heard the term from Major Greenwood, an influential British physician and epidemiologist.[18] Perhaps Greenwood had encountered the term when he studied outbreaks of swine fever in herds of pigs in the early 1910s.[19] Greenwood, however, does not appear to have used the concept in a publication before 1925, when he and Topley complained that in "immunological, as in clinical studies, the great majority of investigators have been so occupied with the individual that they have neglected the herd." Echoing Salmon's criticism of Pasteur's laboratory studies four decades earlier, the pair were critical of the work of "modern experimenters in the laboratory" who, though having "elucidated many particular problems of immunity and susceptibility," had "not given a bird's-eye view of the course of events in an epidemiological unit, a herd."[20] Irrespective of precisely when it was adopted, the concept of herd immunity was embraced by British scientists to close the gap between immunological studies of the individual and epidemiological research on populations.

In the interwar era, the problem of immunity in collectives became particularly appealing to British epidemiologists attracted to an ecological interpretation of disease. Historian J. Andrew Mendelsohn demonstrated that, in the early 20th century, notions of equilibrium came to challenge the often myopic focus of bacteriology on pathogens.[21] Similarly, historian Warwick Anderson notes that during this era "an ecological perspective on infectious diseases sought a means to relate *micro*biological processes to larger environmental or biological forces" thereby capturing "the interactive, dynamic relationships between host and parasite and physical milieu."[22] In the context of an emergent interest in the ecology of infectious disease, herd immunity was often drawn upon to articulate the equilibrium of host, parasite, and environment.

The most prolific scientist to advance an ecological vision of herd immunity was the British Surgeon Commander Sheldon Francis Dudley. Professor of Pathology and Lecturer in Tropical Diseases at the Royal Naval College, Greenwich, Dudley, born of a Quaker family, was attracted to the term because it suited his ecological approach to studying disease.[23] In 1929, he argued that "the ecological point of view" conceptualized "epidemics as manifestations of a loss of balance between the mutual adjustment of host and parasite." He envisioned public health as a form of "applied ecology . . . based on the study of the mutual relationships between man, other living organisms, and the environments they occupy, and the way these relationships affect human health."[24] Elsewhere he argued that the "amount of disease in a community is a function of the herd immunity, the type of infecting parasite, and the character of the environment."[25] By 1936, he was declaring that "scientific epidemiology is medical ecology."[26] For scientists deploying the concept in the interwar period, herd immunity captured the dynamic, unstable equilibrium between humans and other organisms in an unavoidably shared environment.

Emerging in an era before widespread vaccination, retention of the word "herd" signified more than a linguistic relic from the concept's days in the paddock. It captured the disease burdens facing specific subgroups of the population, making it possible to think of collectives as having acquired "immunity," understood to be a balance between host and pathogen. Foreshadowing similar concerns voiced today, Dudley pointed out that "the term 'herd' has been criticized as out of place when applied to human beings," yet he defended its use because it was not coterminous with the population at large but identified subgroups for targeted interventions. "When we pass from the family to the institution, ship, or barracks," he wrote, "it becomes more obvious that the primary duty of the herd doctor is to keep his herd in as high a degree of health as possible." A seaman seemingly recovered from tuberculosis, for example, was best isolated from the rest of the crew (his "herd"), as it would not be wise "to let him return to the mess decks and risk his relapsing and infecting others."[27] Dudley regularly utilized the concept in his studies of diphtheria among British schoolchildren,[28] probably the most common social group to have this term applied to them in the interwar era.

Speaking before the British Medical Association in 1927, physician Graham Forbes discussed his research on diphtheria among schoolchildren. Paradoxically, Forbes argued that, among poorer schoolchildren, overcrowded housing conditions could mitigate the damage caused by diphtheria, keeping its transmission "in check by the degree of herd immunity maintained by repeated exposure to small doses of infection." This was only the case, however, up to a certain point, as "the more crowded the rooms, the greater the risk of close contact with massive infection capable of overcoming acquired partial immunity."[29] In Forbes's analysis, the environment shaped the degree and intensity of exposure to a pathogen, conditioning the group's resistance to serious disease. Other physicians speculated that a common test for immunity to diphtheria—the Schick test—elicited temporary immunity, which, when prevalent among enough schoolchildren, could confer partial immunity in an otherwise susceptible group.[30] For these scientists, herd immunity signaled an equilibrium preferable to the likely outcome of having a group of children entirely susceptible to diphtheria, a condition conducive to an epidemic. Herd immunity did not mean that outbreaks would not recur; nor did it describe a specific quantity of immunity. Rather, it underlined an ecological balance struck between host and pathogen, a balance that was dependent on some degree of continued population exposure.

This ecological vision of herd immunity as an equilibrium reached between a host and a pathogen sharing an environment came to inform decades of research on influenza. As early as 1929, the *Chicago Daily Tribune* paraphrased Dudley's interpretation of the 1918–1919 influenza pandemic as "a by-product of the more than 4 years of world war" during which time "the infection gained virulence and the mass of people lost herd immunity."[31]

In 1951, Irish virologist Patrick Meenan, who would soon collaborate with Albert Sabin and Jonas Salk on their polio vaccines, and coauthor M. Clarke attributed the recent influenza epidemic in Ireland to the diminished "degree of herd immunity" following more than a decade without an epidemic.[32] Two years later, British virologist Christopher Andrewes, then head of the World Influenza Center overseen by the World Health Organization, noted the relationship between the capacity of influenza to rapidly mutate and the adaptability of its host population's immunity:

> Over a period of years, variations may be played upon one antigenic theme, but after some time the possibilities will be exhausted (the herd will be generally resistant to closely related variants), and the introduction of a new motif will be necessary to keep things alive.

An important determinant of influenza outbreaks was "the immunity-level of the population," and it was "doubtless a rise in this which determines the end of an outbreak."[33] Later that decade, during the so-called "Asian flu" pandemic of 1957, the American microbiologist Maurice Hilleman explained to the *Baltimore Sun* that, following mutation of the influenza virus, "there is a loss of 'herd immunity' because the population has not encountered this virus, nor anything sufficiently similar to it, to develop immunities."[34] Nearly half a century later, following an illustrious career in which he helped develop several vaccines,[35] Hilleman noted that "Influenza viruses travel rapidly and induce herd immunity, requiring the virus to mutate and change its antigenic specificity to continue to infect."[36] Continuing to think of herd immunity as an ecological equilibrium, scientists in the second half of the 20th century advanced the concept to explain the interaction between the evolutionary adaptations of influenza, the development and fading of host immunity, and seasonal outbreaks.

MASS VACCINATION AND THE PROBLEM OF HETEROGENEITY

As is clear from the careers of scientists like Hilleman, the concept of herd immunity was not irrelevant to diseases for which immunizing agents existed. By the early 1930s, Topley was investigating the contribution of naturally acquired versus artificially induced immunity among his unfortunate mice populations, and Dudley referred specifically to the value of smallpox vaccination among naval "herds."[37] The analysis of herd immunity arising from infection was sometimes crucial to understanding the viability of vaccination. A 1948 article in *The Lancet* argued that if natural immunity to an influenza strain "lasts only a few weeks," as suggested by animal studies, then "artificial immunization must be relatively hopeless." If, on the other hand, "the duration of immunity for a human herd is really as long as 4 years, possibly because herd immunity is far more complex than the summation of individual host resistances, then there is some hope for artificial immunization."[38] Indeed, recognition of the collective benefits of herd immunity arising from low-level diphtheria exposure was leveraged by British public health experts advocating state-funded immunization in the 1920s.[39]

The expansion of mass vaccination as a public health strategy following World War II produced further diversity in formulations of herd immunity. As vaccines against diseases such as whooping cough (1940s), polio (1950s), and measles (1960s) were developed, and mass vaccination became a crucial pillar of the public health landscape, the concept came to indicate a targeted percentage of immunity induced within a population.[40] Jonas Salk captured the rising optimism for vaccination and its implications for the concept of herd immunity when, speaking before the Royal Society of Health about his polio vaccine in 1959, he claimed that emerging vaccines "will make it possible to bring under effective control . . . many of the viral pathogens." Reporting Salk's speech, the *Daily Boston Globe* suggested that "Salk Expects Herd Immunity From Vaccine."[41]

In fact, Salk does not appear to have used the term herd immunity but, rather, suggested that "application of a vaccine to a sufficient segment of the population should induce what is usually referred to as a herd effect."[42] Obviously not the first use of the term, an extensive online search only turned up one earlier reference to "herd effect" pertaining to human infectious disease. This was a comment by Salk himself in relation to vaccination during the 1957 influenza pandemic.[43] Herd effect indicated the indirect protection conferred to those remaining susceptible in a population of increasingly immunized individuals. Salk expanded on the concept in 1963, noting that vaccines "brought about protective effects beyond those attributable to the number of persons who have been vaccinated." He wondered if "in a given population, the number of seedings can be reduced to a point approaching conditions for extinction."[44] Though he formulated this effect as a byproduct of herd immunity, the two terms soon became regularly conflated.[45]

In 1970, dean of the London School of Hygiene and Tropical Medicine

Charles Edward Gordon Smith published a simple model in which the rate of transmission of a pathogen—its *R0*—determined the percentage of immunity required for local elimination.[46] As other scientists quickly highlighted, however, the model entailed a simplification of the population.[47] In Smith's model, individuals were designated as either immune or susceptible, an understanding that was very different from earlier notions of "resistance." Moreover, the model did not address differences in the social interactions of individuals, meaning it did not account for variations in an individual's contribution to transmission.[48] While it offered clear guidance for vaccination strategies against known diseases, it was not intended to articulate the population dynamics of immunity acquired through infection, a field of research that continues to draw upon older formulations of herd immunity.[49]

As global vaccination programs expanded in the 1980s and 1990s, the conceptual connection between herd immunity and vaccination tightened. Research in the field modeled the complexity of the effects of vaccines in heterogenous populations. Two of the most prolific scientists in this field, Robert May and Roy Anderson, designed complex mathematical models incorporating such considerations as

> the demography of the host population, the duration of acquired immunity and maternally derived protection, age-related changes in the degree of intimacy of contacts among people, and the prevailing levels of genetic, spatial and behavioural heterogeneity in susceptibility/resistance to infection.

The heterogeneity of different populations meant it was "not necessary to vaccinate everyone within a community to eliminate infection; the level of herd immunity must simply be sufficient to reduce the susceptible fraction below the critical point."[50] As mass vaccination aided global efforts to control infectious diseases, scientists again strove to fashion notions of immunity that could account for the variation of human populations.

CONCLUSION

For more than a century, scientists have struggled to formulate the individualistic concept of immunity as one pertaining to collectives. Responses to this tension have sometimes involved thinking of immunity as vitality or resistance. Other times, they have complicated the notion of population, conceptualizing a herd structure or modeling heterogeneity. Whether it was the triad of host–parasite–environment embraced by disease ecologists, or Potter's contrast of the "mode of living" of the range cow versus the dairy cow, accounting for the environment has always been important in scientific efforts to think of populations as "immune." This article has attempted to do justice to the depth of the concept. Much of the public discussion during the ongoing pandemic has focused on the merits of obtaining herd immunity via natural infection. Yet precise definitions of what that condition equates to are rarely being made explicit. This history suggests three ways such discussions may benefit by acknowledging the complexity of this crucial concept.

First, the ambiguous nature of the term is resulting in different, at times conflicting, applications during the pandemic. Scientists sometimes make opposing claims while not clarifying the precise understanding they are invoking, such as its meaning vis-à-vis mass vaccination and disease elimination[51] versus that pertaining to the process by which a novel pathogen becomes endemic.[52] As this article has demonstrated, throughout its history, the concept has referred to both of these formulations. The problem is not that some are using the term correctly and others not, but that precisely what understanding of an "immune" population is being invoked is not always being made explicit.

Second, the overwhelming focus of the public discussion on what percentage of immunity is required before herd immunity is attained has simplified the complexities of the concept, detracting from its possible insights.[53] Scientific efforts to analyze the role of population heterogeneity to the trajectory of the pandemic have received little public discussion.[54] From Salmon's emphasis on a wholesome diet to Anderson and May's efforts to model heterogeneity, scientists have long considered a population's resistance to disease as more comprehensive than a percentage of individuals with antibodies.

Lastly, while the arrival of vaccines may appear to make deeper consideration of the concept redundant, the distribution and delivery of limited resources raises the perpetual problem of herd immunity: how to realize immunity most effectively in a population. Should vaccines that were assessed in double-dose trials be given as single shots to twice the number of people?[55] Is wider dissemination of partial immunity preferable to that which is more robust, but less widely dispersed?[56] Should states vaccinate the portion of the population at greatest risk of serious disease[57] or focus on creating the greatest quantity of immunity in their population?[58] Recognizing the complexities of this

concept may help us actualize the most effective and egalitarian distribution of immunity across the population. Ultimately, how we achieve this will define how our era resolves the ongoing conundrum of herd immunity. AJPH

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CONFLICTS OF INTEREST

The author has no conflicts of interest to declare.

ENDNOTES

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