Parasitic diseases of humans and livestock are ubiquitous in the developing world and have substantial impacts on human well-being. For the estimated one billion people living in poverty who rely on livestock for their livelihoods, parasites steal valuable nutritional resources through multiple pathways. This diversion of nutrients ultimately contributes to chronic malnutrition, greater human disease burdens, and decreased productivity of both humans and livestock.

The past 15 years have borne witness to unprecedented improvements in health conditions among developing countries. Catalyzed partly by the HIV pandemic around the turn of the 21st century, the global health agenda has evolved from narrowly focused ‘vertical’ initiatives, such as the Global Fund to Fight AIDS, TB, and Malaria, to a more integrated agenda for improving health systems, as codified by the WHO’s six ‘building blocks’ of health-system strengthening. Support for these efforts was critically bolstered by a growing understanding of their role in broader strategies for economic development, advanced by the Millennium Developments Goals. However, even as the global health movement becomes integrated with systems of healthcare in developing countries, there remain substantial blind spots on how these systems of healthcare interface with complex systems of disease.

Over two billion people still live in poverty (<US$2 per day) and 800 million experience chronic undernutrition (http://r4d.dfid.gov.uk/Output/190314/). Physical and economic barriers to food access and availability, and the resulting hunger and malnourishment, can have a profound impact on human health and economic productivity. Protein-energy malnutrition, or inadequacy calorie and/or protein intake, inhibits long-term physical and cognitive development, and contributes to half of all deaths in children under the age of 5 years [2]. Deficiencies in micronutrients, such as iron and vitamin A, cause debilitating conditions, including anemia and blindness in millions of people, and increase the risk of preterm birth and maternal death [3]. These health outcomes ultimately affect income-generating potential of individuals and, therefore, the economic security of households and communities.

Malnutrition among the poor is generally caused by two forces: (i) inadequate acquisition of nutrients, often due to a lack of access to nutrient-dense foods; and (ii) inhibited uptake or depletion of nutrients due to disease, most often in the form of parasites [4]. While the global health community recognizes that human parasites have an important influence on human health, nutrition, and economic productivity, there is considerably less research on the pathways through which livestock parasites may induce similar outcomes. After all, nearly half of the world’s poor rely on domestic livestock to support their economic and nutritional needs (http://r4d.dfid.gov.uk/Output/190314/). Livestock production is undermined by parasitic diseases, which inherently compete for scarce resources [5]. Thus, livestock parasites may reinforce traps of poverty, malnutrition, and disease in ways that are directly comparable to human diseases. A better understanding of these relationships can inform the important work of livestock policy initiatives such as those advanced by the World Organisation for Animal Health (www.oie.int), the International Livestock Research Institute (www/ilri.org), and Vétérinaires sans Frontières (vsf-international.org), among others, to further develop integrated livestock health strategies targeted for poverty reduction.

To understand these relationships, Figure 1 presents a schematic of a coupled system of human health, livestock disease, and economic productivity, which corresponds to model results in Figure 2. In such systems, economists model income generation as a production process, where ‘capital’ is combined with labor to produce goods, such as food in a subsistence economy (Figure 1, green lines). Capital can be broadly defined as various forms of durable assets that are used to produce benefits over time; and includes physical capital (equipment), natural resources (land), and human capital (knowledge, skills, or health status) [6,7]. For the one billion poor livestock keepers in the world, livestock have a fundamental role in this production process (http://r4d.dfid.gov.uk/Output/190314/). Animals and animal products (meat, eggs, and milk) are sold in local markets to generate income or are available as food for consumption [8]. Livestock can also serve as a direct form of physical capital when used for draught power or when manure is used to improve soil fertility and increase crop production [8].

Given that healthy humans are an important part of this production process (Figure 1, red lines) [6], parasitic diseases that impact human health lower economic productivity and reduce wealth accumulation, which further undermines health status. Livestock serve as another living form of capital in the system, and so the burden of livestock parasites is an extension of that of human parasitic disease. Given the multiple indirect pathways by which livestock contribute to economic production, nonzoonotic livestock parasites (which represent most livestock parasites) and livestock health strategies.
parasites) may be even more important to human health than zoonotic parasites, such as echinococcosis, foodborne trematodiasis, cysticercosis, and zoonotic schistosomiasis [9], that contribute directly to human disease [10].

The system described by Figure 1 can be explicitly modeled by coupling existing models of disease, livestock, and economic dynamics, variations of which have been presented elsewhere [11,12]. For heuristic purposes, Figure 2 presents the results of a stylized version of this system where both zoonotic and nonzoonotic livestock diseases are shown to influence human disease prevalence and income. The key features of such models are that the various forms of capital are used for generating income, and that income is in turn used to accumulate capital and reduce human disease (by decreasing exposure or increasing rates of recovery or treatment). As the transmission of livestock diseases rise (Figure 2, left-hand column), the prevalence of human disease increases in the presence of both zoonotic and nonzoonotic disease (Figure 2C), while income is lost (Figure 2E). Conversely, as rates of clearance (or recovery) of livestock disease increase, the prevalence of human disease falls (Figure 2D) and income rises (Figure 2F). While these are only theoretical results, rather than empirical estimates, they provide a formal foundation for how livestock parasites influence such systems through multiple pathways that are comparable to human parasites. They also provide simple implications for policy interventions that reduce livestock disease transmission or increase rates of disease clearance.

Given the clear importance of livestock health on human wellbeing and economic

Figure 1. The Impact of Parasites on Human and Livestock Health, and Economic Productivity. The health of humans and livestock (in red) directly impacts their capacity to contribute to economic production (in green). Economic production is the process by which inputs in the form of human capital, physical capital, and natural resources are used to generate outputs in the form of income, food, and other economic goods. These outputs can be re-invested to generate wealth when economic productivity is high. In these systems, human health and livestock are important forms of human and physical capital respectively. Animals and animal products contribute as both inputs and outputs of the production system. Parasitic diseases (in blue) impact human and animal health, and reduce economic production through multiple pathways. When economic production is severely affected, wealth cannot accumulate and the ultimate result is persistent poverty and disease.
development [10,13], can lessons from global health be expanded to improve the delivery of animal health services to the poor? Just as for human disease, there are well-known tools for livestock disease prevention and control, including vaccines and chemotherapeutic agents, but they are generally underutilized by the poor, because they are often not available, are cost prohibitive, or undervalued [10]. Although the burden of livestock disease is determined by population-level processes, the cost of control remains largely in the private realm, where the financial burden falls heavily on the individual livestock producers [10].

Historically, the treatment of human diseases has faced similar challenges.

However, for many of the major diseases of poverty, control programs have been established at national or region levels, and are increasingly financially supported by governments and international organizations [14]. For example, control programs for soil-transmitted helminths and schistosomiasis are often based on well-defined treatment protocols developed by the WHO and are designed around the scheduled use of prophylactic chemotherapy in preschool and school-aged children (i.e., mass drug administration) [14]. This population-level approach is designed to target humans who are most susceptible to the effects of malnutrition and parasitic infection, and remove the financial barriers to treatment.

Similarly, providing animal health services at the population level, rather than simply at the level of the individual herd or flock for those who can afford them, ensures that services are delivered to those who have the most to gain from improvements in livestock productivity: the poor and chronically malnourished. Identifying current programs that take this approach and scaling them to reach target populations will require financial buy-in from the global health and development community and necessitate improvements in veterinary health systems. The design of such programs for livestock parasitic diseases necessitates further research, perhaps similar to that of recent studies for human parasite control [15], to determine best practices for the administration of...
anthelmintic drugs and incorporation of animal management practices that minimize drug resistance and achieve sustainable results. Ultimately, poor communities would benefit from integrated human and animal health services, where disease and poverty are tackled simultaneously through multiple pathways.

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References

Letter
Born to be Wild – Don’t Forget the Invertebrates
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Parasitology research mostly aims to control parasites of humans and domesticated animals. Recently, many scientists have realized much can be learned by studying wildlife parasites. To this end, Trends in Parasitology published two special issues comprising some of the most interesting, topical science relating to wildlife parasitology [1]. The emphasis of the published articles was almost exclusively on parasites that use vertebrate animal hosts. Here, we argue that progress in parasitology could be accelerated if more parasitologists studied parasites that use invertebrates as definitive hosts.

High Diversity Means Better Model Systems
The diversity of invertebrate animals is vast compared with vertebrates. According to a recent study, the phylum Craniata (vertebrates) comprises 64,832 species, a mere 4% of total animal biodiversity [2]. This probably represents a substantial overestimate as it is likely there are many more undescribed invertebrate than vertebrate species. In spite of this, most animal biologists work with vertebrate animals and this phenomenon has been referred to as ‘institutionalised Vertebratism’ [3]. Most invertebrate animals have parasites and their great diversity enables identification of individual host–parasite systems ideal for studying specific areas of fundamental parasitology. However, while the lack of taxonomic expertise for parasites of vertebrates has been noted [4], the situation is even worse for the invertebrates.

The Evolution of Parasitism
A theme frequently addressed by parasitologists is determining the genetic changes associated with adopting a parasitic lifestyle. Parasitologists often compare genomes of their preferred parasite with the model nematode, Caenorhabditis elegans, even though the two organisms may be dissimilar. An excellent comparative model would be the facilitative slug parasitic nematode Phasmarhabditis hermaphrodita and C. elegans. The nematodes are closely related phylogenetically, feed on decaying plant material, and dauer larvae of both associate with slugs. However, whereas C. elegans merely uses slugs for transport (phoresy), dauer larvae of P. hermaphrodita have the ability to develop and feed on slug tissue [5]. The nematodes are a particularly rich source of invertebrate parasites that infect many taxa. The evolutionary relationships and the suggestion that certain vertebrate parasites may have evolved via invertebrate parasitism makes them particularly worthy of study [6] (Figure 1).

Dynamics of Coinfection
Another topic considered by wildlife parasitologists is coinfection and, to this end, Rynkiewicz et al., consider the applicability of ecosystem ecology tools for parasitology [7]. Because the diversity of macroparasites of vertebrate animals is limited, these authors considered all pathogenic microorganisms as parasites, necessitating study of the whole host–microbiome, which the authors admitted could result in ‘potentially overwhelming levels of complexity’. It should be noted that most ecosystem ecology has been developed using macroflora and fauna. An ideal model for studying ecosystem tools for coinfection could be the spiribolid and spirostreptid millipedes. These invertebrates have a relatively simple anatomy, but support a surprising diversity of macroparasites [8], and we have observed up to ten parasite species cohabiting in a single host millipede.

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