

between temperature, development rates and life histories. Nick Dulvy (University of East Anglia, Norwich, UK) showed that species of sharks and rays in which females provide postfertilization nutrients to embryos are always found in warm waters. He attributed this to a need for tropical species to make up for a shortfall in embryonic energy as a result of lower conversion efficiency at high temperatures. Daniel Pauly (University of British Columbia, Vancouver, Canada) went further, using a broad theory to explain why tropical species tend to be smaller than temperate ones. At high temperatures, fish grow quickly and therefore require more oxygen, but oxygen uptake might be limited by gill area. Thus, higher growth is offset by smaller body size as a means

of reducing metabolic demands. Although the generality of this mechanism was questioned during a lively debate, it does provide a thought-provoking interface between constraint and adaptation in the evolution of life histories of fishes.

Perhaps the life history connections with warm temperatures will ultimately distinguish tropical fishes from others, but this conference made it clear that tropical fish are not a homogeneous group. With habitats ranging from African rift lakes to coral reefs and open oceans, how could they be? Our overall impression was that this meeting effectively brought out the fact that some of the best examples of species explosions and extinctions are from the tropics, but the processes involved are themselves not uniquely tropical.

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Wildlife disease ecology: from theory to policy

The study of wildlife diseases has traditionally been viewed as a rather esoteric subject pursued by a disparate collection of individuals working mainly in the veterinary sciences. However, in the past 20 years, there has been a realization that the study of wildlife diseases is relevant to a wide range of disciplines, including conservation biology, public health, evolutionary biology and mainstream ecology^{1–3}. This breadth of interest was clearly evident in presentations and discussions at the recent Wildlife Diseases Workshop at the Centro di Ecologia Alpina in Trento, Italy in July [organized by Peter Hudson (University of Stirling, UK) and Annapaola Rizzoli (Centro di Ecologia Alpina, Trento, Italy)]. Its aims were to identify advances made in the study of wildlife diseases since a previous gathering at the Newton Institute in Cambridge, UK, in 1993 (Ref. 4), and to provide directions for research over the next five years.

The workshop brought together experts in mathematics, genetics, immunology and ecology, whose presentations ranged in scale from the molecular to the community level. The importance of pathogens in shaping ecological communities was discussed by Andy Dobson (Princeton University, USA), who argued that since fungal pathogens in tropical rainforests can reduce the recruitment of conspecifics adjacent to parent trees, they might give an advantage to rare tree species (analogous to the Janzen–Connell effect⁵). A main focus of the meeting,

however, was the converse of this – the threat that disease poses to wildlife diversity.

Wildlife disease management

Rosie Woodroffe (University of Cambridge, UK) listed a range of endangered species that are threatened by parasites and pathogens (Table 1), and reviewed the intervention strategies potentially available to conservation biologists to minimize this threat, including vaccination, treatment, reduction of contact with disease reservoirs and the management of population size and structure. She argued that appropriate decisions regarding management strategies can only be made with significant inputs from epidemiologists. This point was echoed by George Hess (North Carolina State University, USA), who discussed the merits of using corridors to link fragmented populations, a management strategy promoted by conservation biologists. He argued that this could either benefit endangered species by reducing the risk of local extinction, or could threaten them by increasing the rate of disease transmission – the outcome would be strongly dependent on the nature of the pathogens involved.

Sarah Cleaveland (University of Edinburgh, UK) reported on the efficacy of vaccinating domestic dogs (in an experiment in northern Tanzania) as a measure for controlling rabies and canine distemper in threatened wildlife. Preliminary results suggest that although vaccination

coverage was slightly lower than the 70% theoretically required to eliminate these diseases, there has already been a dramatic decline in the incidence of rabies in domestic dog populations in vaccinated villages. Rabies cases continue to be reported in adjacent wildlife populations, but it is too early to determine whether the virus can persist in wildlife reservoirs independently of dogs. She suggested that because unit costs of vaccination decline with increasing size of village, and because some villages contribute to infection more than others, targeting of vaccination could substantially improve the cost-effectiveness of disease control. However, as Chris Dye (World Health Organization, Basel, Switzerland) pointed out, the decision about which management programme to employ is often made by politicians rather than scientists. Ecologists therefore have an obligation to interact with policy makers and to ensure that the results of their research are understood by those making the decisions. Debate about the merits and difficulties of interacting with policy makers, and addressing applied questions, continued throughout the workshop.

Host–parasite interactions

Wildlife diseases often involve complex interactions, as exemplified by the contribution of Gary Smith (University of Pennsylvania, USA), who described the diversity of transmission routes and multi-species associations of tick-transmitted Lyme borreliosis in the USA. Two further examples of tick-borne diseases illustrated how complexity in pathogen transmission can help maintain disease within wildlife populations. Sarah Randolph (Oxford University, UK) noted how the persistence of tick-borne encephalitis

Table 1. Species for which diseases have been implicated in population extinctions and near-extinctions^a

Host	Origin	Pathogen	Source of infection
Black-footed ferret (<i>Mustela nigripes</i>)	North America	Canine distemper virus	Badgers (<i>Taxidea taxus</i>) and coyotes (<i>Canis latrans</i>)
Bighorn sheep (<i>Ovis canadensis</i>)	North America	<i>Pasteurella</i> and scabies (<i>Psoroptes</i>)	Domestic sheep
African wild dog (<i>Lycan pictus</i>)	Masaai Mara-Serengeti	Rabies	Domestic dogs and black-backed jackals (<i>Canis mesomelas</i>)
Ethiopian wolf (<i>Canis simensis</i>)	Ethiopia	Rabies and canine distemper virus	Domestic dogs
Blanford's fox (<i>Vulpes cana</i>)	Israel	Rabies	Red foxes (<i>Vulpes vulpes</i>)
Mednyi arctic fox (<i>Alopex lagopus semenovi</i>)	Aleutian Islands	Mange	Domestic dogs
Monk seals (<i>Monachus monachus</i>)	Mediterranean	Morbillivirus	Dolphins (<i>Stenella coeruleoalba</i>)
Thylacine (<i>Thylacine cynocephalus</i>)	Tasmania	Canine distemper virus	Domestic dogs
Indian wild ass (<i>Equus hemionus khur</i>)	India	African horse sickness and surra (<i>Trypanosoma evansi</i>)	Mosquitoes (<i>Culicidae</i>) and horseflies (<i>Tabanidae</i>)
Hawaiian crow (<i>Corvus hawaiiensis</i>)	Hawaii	Malaria (<i>Plasmodium relictum</i>) avian pox	Introduced bird species
Heath hen (<i>Tympanuchus cupido cupido</i>)	North America	Blackhead (<i>Histomonas elegridis</i> / <i>Heterakis gallinarum</i>)	Domestic turkeys

^aNote that in many of these cases the role of disease is uncertain or disputed. The information is compiled from various sources; ask authors for details.

(TBE) could not be explained by tick-to-tick transmission of the virus via systemic infections alone (those where the virus multiplies inside the host). However, viral persistence was attained after the inclusion of nonsystemic transmission between ticks co-feeding on the same host individual⁶. A similar role for nonsystemic transmission between co-feeding ticks has been implicated in the persistence of louping-ill virus in red grouse (*Lagopus l. scoticus*) populations in Scotland. Models presented by Rachel Norman (University of Stirling, UK) suggested that the virus could persist even when the only reservoir was a population of a nonviraemic host (the mountain hare, *Lepus timidus*).

Several speakers at the workshop discussed the mechanisms that can generate heterogeneities in host-parasite interactions. For example, Ken Wilson (University of Stirling, UK) emphasized the importance of host age and sex in determining nematode worm burdens in Soay sheep (*Ovis aries*) on St Kilda. He also discussed recent results linking genes at the major histocompatibility complex (MHC) with enhanced parasite resistance and overwinter survival⁷. The role of host genetics in epidemiology was further stressed by Mark Woolhouse (University of Edinburgh, UK), who reported on a model of scrapie dynamics in a flock of domestic sheep⁸. He emphasized that a full understanding of the disease dynamics could be attained only after the inclusion of a known genetic component to the susceptibility to infection. This observation is important because one method of reducing the impact of scrapie in domestic sheep is to introduce new stock from genetically distinct flocks. However, if the new stock carries genes for susceptibility to scrapie, their introduction might actually facilitate disease

transmission. This result could have important implications for reintroductions to small populations of endangered wildlife.

Genetic variation is not restricted to the host population. Bill Amos (University of Cambridge, UK) reported on a recent study of nematode worms in which it was shown that there was just as much genetic variation within parasite populations as there was between them. However, Andrew Read (University of Edinburgh, UK) argued that there was little evidence to suggest that this genetic variation has much influence on the parasite's transmission efficiency. This situation contrasts with that for microparasites, such as malaria, where there is growing evidence that the transmission rate of mixed-clone infections is greater than that of single-clone infections, despite the fact that the total number of parasites produced does not differ⁹.

Recent theoretical advances

Over the past five years, since the previous meeting at the Newton Institute, models of host-parasite interactions have become biologically more realistic. Hans Heesterbeek (Centre for Biometry, Wageningen, The Netherlands) discussed how to estimate the basic reproduction number (R_0) for macroparasites in seasonal environments, whilst Jonathan Swinton (University of Cambridge, UK), advocated the use of critical metapopulation distributions (as opposed to critical community sizes) for determining thresholds for disease persistence in fragmented populations of wildlife hosts. He demonstrated the usefulness of this concept in understanding the 1988 phocine distemper virus epidemic in harbour seals (*Phoca vitulina*)¹⁰.

One of the major discussion points of the Newton Institute meeting was the

difficulty in modelling multihost, multi-pathogen interactions³. At the Trento workshop, Jon Greenman (University of Stirling, UK) demonstrated the use of a bifurcation mapping technique, known as Gateway Analysis², which avoids intractable algebraic problems and allows the analysis of interactions between multiple host and parasite species. Other participants at the workshop were concerned with testing the basic assumptions of the models being used and developing new statistical methods for their analysis. For example, Mike Begon (University of Liverpool, UK) used data on the prevalence of cowpox virus in bank voles (*Clethrionomys glareolus*) to test a fundamental premise of host-pathogen models known as the mass action assumption, whilst Roberto Rosa and Stefano Merler (Centro di Ecologia Alpina) discussed the application of Bayesian and tree-based methods to the study of wildlife diseases.

Prospects

Despite advances in the modelling and statistical analysis of infections of wildlife, there was a general consensus at the workshop that the gap between theory and solid experimental evidence had widened over the past five years. For example, there are still very few examples where the regulation of a host population by parasites has been convincingly demonstrated. Perhaps the best experiment to date that illustrates host regulation in the wild was presented at the workshop by Dave Newborn (Game Conservancy Trust, Gunnerside, UK). He showed that the cyclic crashes of red grouse could be prevented by removing their gastrointestinal nematodes using anthelmintic treatment, clearly demonstrating that parasites are the driving force behind the cycles.

The workshop ended with a series of 'visions', designed to provide direction for host-parasite research over the next five years. Perhaps the most notable of these was presented by Andrew Read on genetics and evolution, who commented that the checklist for future evolutionary research that was provided at the end of the 1993 meeting⁴ still largely holds today. This list contained elements, such as determining the epidemiological consequences of genetic variation, where remarkably little progress has been made over the past five years. Angela McLean (Institute of Animal Health, Compton, UK) pointed out that many of the genetic and immunological techniques required for such studies have already been developed; they are just not yet being used by epidemiologists and evolutionary ecologists.

Final comments at the workshop concerned the role of ecology in the new millennium. Andy Dobson's view was that whereas the physical sciences took the lead role in solving many of the major problems of the 20th century, the biological sciences will be far more important in addressing the environmental threats facing us in the next century. From a wildlife disease perspective, continually

increasing levels of global movement will invariably lead to greater disease transmission both within and between host species. Climate change could also lead to a general increase and spread of pathogens into new areas, as environmental conditions become more favourable for disease transmission. Extinctions caused by disease will serve only to exacerbate reductions in biological diversity (arguably the most irreplaceable of global resources), alter ecosystem functioning, and have profound evolutionary consequences for the communities involved. Given that these future problems are too complex for simple politics, increasing education of the policy makers and the public would seem a logical priority.

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Paleoecology meets ecology on questions of scale

Ecologists and paleoecologists might seem to have little in common: ecologists study live organisms, paleoecologists dead ones. Ecologists study interactions between organisms over relatively brief periods, which are much shorter than the duration of species and often shorter than an individual's lifetime. Paleoecologists study processes acting over long periods, during which historical accidents, tectonic movements and evolution influence the distribution of species. This dichotomy breaks down on scrutiny. Ecologists studying species interactions over large spatial scales (e.g. regional or continental scales) often find historical influences on species distributions, and thus ecologists can infer processes acting across 'deep time' by sampling in 'wide space'^{1,2}. Across geological time, paleontologists have found that the dynamics of large numbers of taxa often conform to the expectations of simple ecological models³. Paleoecologists are not confined to deep time, because some behaviors that occur during

the lifetime of an individual (e.g. worm burrows, tooth wear and predator borings) leave traces in the fossil record⁴.

In May this year, at Solomons, MD, USA, a multidisciplinary group representing both fields⁵ convened a Geological Society of America (GSA) Penrose Conference, cosponsored by the Paleontological Society and the Ecological Society of America, to explore the importance of scale in ecology and paleoecology. The conveners posed the question: 'how is our understanding of the forces governing species distributions affected by the temporal and spatial scale at which data are collected and analysed?'

Effects of temporal scale

The largest obstacle in comparing ecological and paleoecological data is the difference in temporal resolution. Paleontological data, such as species associations at fossil localities, are typically 'time averaged'. Fossil assemblages require time to accumulate and deposit fossils in a given

location, and if time averaging has been severe, then the remains of species that did not coexist can potentially become combined into the same assemblage. However, Mike Rosenzweig (University of Arizona, Tucson, USA) reminded the participants that ecological data are also time averaged, in the sense that they are recorded against some measure of sampling effort (e.g. species richness is measured within a given area over a given time). A certain amount of 'time averaging' is actually necessary to obtain a representative sample of a community (a set of species living together in space and time), because averaging dampens the effects of short-term fluctuations in species composition.

Not all fossil assemblages are severely time averaged. Russ Graham (Denver Museum of Natural History, USA) pointed out the existence of bone assemblages in Quaternary wolf dens that had accumulated in less than 50 years (measured by high resolution dating techniques). Species associations can be inferred from such sites with a greater degree of confidence than is usually possible in paleontology⁶. Therefore, it seems that ecology and paleoecology share the tradeoffs associated with time averaging, and that the degree to which time can be resolved in the