What makes a specialist special?

Two centuries ago, fleas were feasting on the blood of passenger pigeons (*Ectopistes migratorius*), the most abundant birds in North America[1]. One hundred years on, Martha, the last passenger pigeon, took her final breath, and the fleas' fate was sealed. This popular, and possibly apocryphal, tale has been used to illustrate how 'running out of niche' leads to unavoidable extinctions[2]. However, this process begs an obvious question: why were the fleas stuck with the doomed pigeons?

The factors that constrain niche expansion lie at the heart of a key problem in evolutionary ecology: why are there so many different types of species? Why is there not an ultimate organism adapted to exploit all ecological niches? Host–parasite systems provide fertile – and important – ground for examining these questions: habitat specificity can be readily defined (i.e. number of host species exploited), and host specificity varies, even among closely related taxa (e.g. Ref. 3). A new study of cave swiftlets (*Aerodramus* and *Collocalia* genera) and their parasitic feather lice (*Dennyus*) by Tompkins and Clayton[4] illustrates both the potential and the challenges of investigating the determinants of host specificity.

Host specificity

Why are there no parasite species exploiting all the members of large taxa such as mammals or birds? Evolutionary ecology offers two major classes of explanation for habitat restriction: limited dispersal and limited adaptation. Some parasites might have a limited host range simply because they do not come in contact with other host species. Perhaps the fleas of passenger pigeons had opportunities to transmit only to other passenger pigeons? Alternatively, host specificity could arise because of adaptive specialization: pigeon fleas might have been incapable of successful reproduction on other avian species.

We have remarkably little understanding of the relative importance of these alternatives in limiting host range in natural parasite populations. However, at least in principle, it is easy to determine in particular cases. If host specificity arises because of limited dispersal, parasites should be capable of proliferating once experimentalists help them over the dispersal barrier. If adaptive constraints are responsible, then parasite fitness will be severely reduced on novel host species.

Lousey swiftlets

Tompkins and Clayton[4] tested these predictions using host-specific species of feather lice from four species of cave swiftlets in Borneo. Their study is unusual in that they exploited natural host–parasite combinations and conducted the experiments in the field. Importantly, they used reciprocal transfer experiments; such experimental designs eliminate the possibility that some host species are simply worse habitat for parasites.

Cave swiftlets, as their name suggests, live in caves. The feather lice they harbour are chewing lice, which are obligate ectoparasites that spend their lives feeding from their hosts. Some species are found almost exclusively on one swiftlet species; others are found on three different host species. Each year, during the bird's breeding season, lice reproduce and their offspring infect the nestlings[5]. Horizontal transmission can also occur if lice crawl between nests. In an elegant experiment, Tompkins and Clayton[4] transplanted host-specific feather lice between nestlings of closely related species of cave swiftlets. The survivorship of lice transferred between species was compared with that of lice transferred to different individuals in the same species.

Louse survival was severely depressed following transfers to novel hosts. Furthermore, surveys of the louse fauna of over 1300 swiftlets turned up the occasional specialist louse on the 'wrong' swiftlet species. Although it is hard to eliminate experimental contamination completely, such observations argue against an absolute lack of dispersal to new host species. Given the poor survivorship of lice on abnormal hosts, limits to adaptation is implicated as the major cause of host specificity in this system.

Correlational evidence points to a possible proximate mechanism. Lice that were transferred to hosts with similar feather barb dimensions did less poorly than those that were moved to more dissimilar species. In addition, those lice that did survive were found at feather positions with the same barb diameter as their usual location on their original host. Apparently, some of the negative effects of host shift can be offset by microhabitat shift. But quite why barb diameter should matter is unclear. Bill morphology suggests that preening is not likely to be a major source of louse mortality. However, adult swiftlets feed on the wing and feather lice must have a hard time clinging on during aerial acrobatics. This problem might also occur in nestlings because vigorous wing flapping is apparently common before fledging. It would be useful to know whether the stresses encountered by lice during such activity generate an optimal morphology (e.g. leg size) for a given barb size. Attachment *per se* need not be involved: microclimate around the lice on the feathers is also likely to be affected by barb size, and many other host features probably covary with barb size, not least body size and the morphological and physiological variation that goes with that.

Constraints on adaptation

Nailing down the relevant proximate mechanism might help address the next key question: what is constraining adaptation in this system? In theory, limits to adaptation can arise by several routes[6–9]. The strength of selection might be insufficient to counter the mutational degradation of alleles conferring benefits in rarely encountered environments, or there might be tradeoffs – a jack-of-all trades might be a master of none. Empirical evidence for any of these ideas is sparse. If legs and barb sizes are involved, it might be possible to determine whether tradeoffs exist in the louse–swiftlet case from aerodynamical principles alone.

Alternatively, it might be the low rates of dispersal between swiftlet species that limit adaptation. If lice were more frequently encountering the 'wrong' host species, they might have adapted to more than one host. One of the lice species in the Borneo cave is frequently found on three swiftlet species, which suggests that the barriers to adaptation revealed by the transplant experiments are not insurmountable. Evolutionary responses to experimental manipulations of dispersal rates between different host species would help, but are probably feasible only in laboratory models.

Prospects

These general issues have implications far outside the traditional remit of evolutionary ecology. By definition, zoonotic disease agents have the ability to cross species boundaries and, as HIV has tragically demonstrated, emergent diseases of biomedical significance are frequently the result of a host switch. How much are we, and the animals we depend on, protected by host specificity? How much of this specificity is due to adaptive specialization? How can we create conditions that inhibit parasite

 0169-5347/99/$ – see front matter PII: S0169-5347(99)01697-3

adaptation to hosts we care about? Even at a proximate level, major questions remain unanswered. For instance, how do host responses to infection vary between host species? Does adaptation to new hosts principally involve evasion of protective host responses or other host-specific physiological conditions? Evolutionary ecologists could be playing a major role in addressing these questions in the biomedical and veterinary context. What keeps parasites host-specific matters at least as much for us as it did for passenger pigeon fleas.

Acknowledgements
We thank Alan Gemmill and Nick Colegrave for insight.

Rebecca Timms
Andrew F. Read

Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh, UK EH9 3JT (r.timms@ed.ac.uk; a.read@ed.ac.uk)

References

1 Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*, Cambridge University Press
2 Willams, G.C. (1975) *Sex and Evolution*, Princeton University Press
3 Anderson, R.C. (1992) *Nematode Parasites of Vertebrates. Their Development and Transmission*, CAB International
4 Tompkins, D.M. and Clayton, D.H. (1999) **Host resources govern the specificity of swiftlet lice: size matters,** *J. Anim. Ecol.* 68, 489–500
5 Lee, P.M.L. and Clayton, D.H. (1995) **Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success,** *Ecol. Entomol.* 20, 43–50
6 Fry, J.D. (1996) **The evolution of host specialisation: are trade-offs overrated?** *Am. Nat.* 148, S84–S107
7 Kawecki, T.J. (1997) **Sympatric speciation via habitat specialization driven by deleterious mutations,** *Evolution* 51, 1749–1761
8 Kawecki, T.J. (1998) **Red Queen meets Santa Rosalia: arms races and the evolution of host specialization in organisms with parasitic lifestyles,** *Am. Nat.* 152, 635–651
9 Whitlock, M.C. (1996) **The Red Queen beats the Jack-of-all Trades: the limitations on the evolution of phenotypic plasticity and niche breadth,** *Am. Nat.* 148, S65–S77

Toxins, nutrient shortages and droughts: the serpentine challenge

Serpentine is the common (and strictly speaking erroneous) name used by biologists for a suite of rock types that contain ferromagnesian minerals. Serpentine is in fact just one of those minerals and the igneous or metamorphic rocks containing them are better designated as ultramafic – a more recent geological term emphasizing their high magnesium (Mg) and iron (Fe) concentrations[1]. These rocks are also often relatively rich in chromium (Cr), cobalt (Co) and nickel (Ni), and have relatively low concentrations of silicon (Si), and usually low concentrations of phosphorus (P), potassium (K) and calcium (Ca). The soils derived from these rocks can offer an edaphic environment with toxic concentrations of Mg and Ni, a dearth of mineral nutrients (including micronutrients), and with a strong tendency to drought and the associated proneness of their vegetation to burning. The soils are very variable but, in their extreme forms, their combination of adverse chemical and physical conditions presents a major challenge to plant growth and hence they can bear open, low-stature vegetation that is floristically distinct with a high proportion of endemic or disjunctly distributed species. They were first recognized as bearing unusual plants by Caesalpino in 1583 (Ref. 2) and a large literature on their plants and soils is available for many countries in the world[3–6].

The biological importance of ultramafics far outweighs the *c.* 1% of the earth's surface they occupy. For example, they can be refuges for whole vegetation types, as is seen in parts of western California where the native grasslands have succumbed to European introductions except on ultramafics, where the exotics have been unable to produce resistant races.

Until this decade, the separate groups of scientists working on the biology of ultramafics had done so with little international contact. This situation was changed by the 'First International Conference on Serpentine Ecology', which was held at Davis, California in 1991 (Ref. 5). A second international conference was held in 1995 in New Caledonia[6] and the third, organized by K. and M-J. Balkiwill, in March this year in South Africa (University of the Witwatersrand, Johannesburg). I am reporting on some of the important features of the third conference.

The conservation importance of ultramafic rocks quickly emerged as a major theme of the conference and it is clear that a high proportion of their endemic plant species must be endangered. Ed Witkowski (University of the Witwatersrand) showed this emphatically using the Swaziland endemic red-hot poker, *Kniphofia umbrina*, as an example, and it was implicit in many of the other presentations, including the elegant work of Roger Reeves (Massey University, New Zealand) *et al.* on the highly fragmented outcrops in western Turkey.

Several papers dealt with ultramafic soil microbes and Hamid Amir and René Pineau (Université Française du Pacifique, New Caledonia) demonstrated not only adaptations of free-living microorganisms to high soil Mg, Co, manganese (Mn) and Ni, but also their role in releasing these elements into a plant-available form. Mycorrhizas were briefly dealt with, but we await critical experiments before an assessment can be made of their possible roles in ultramafic resistance. Certainly the Brassicaceae and Caryophyllaceae, two predominantly non-mycorrhizal families, are a conspicuous component of many ultramafics at higher latitudes in the north temperate zone.

The evolutionary adaptation of plants to ultramafic soils is a crucial aspect of their ecology. Mark Macnair (Exeter University, UK) *et al.* reported some recent work on inherited and correlated traits apparently for drought tolerance and also for ultramafic soil tolerance in five species of the *Mimulus guttatus* (monkey-flower) complex. This is important not only because it shows the genetic component in tolerance, but also because it backs ideas of the role of drought in ultramafic soils. The studies of Anna-Britt Nyberg (Mid Sweden University) *et al.* on *Cerastium alpinum* (Alpine mouse-ear) neatly demonstrated the capacity for independent evolution of ultramafic resistance in different races of this species, which each have a separate genetic background. The existence and importance of soil heterogeneity was highlighted by the detailed studies of Nishanta Rajakaruna and Bruce A. Bohm (University of British Columbia, Canada) on Jasper Ridge, California, who showed the existence of two virtually noncrossing races of *Lasthenia californica* growing on different but juxtaposed ultramafic soils.

The consideration of the physiology and chemistry of organisms on ultramafic

  PII: S0169-5347(99)01698-5