ancient deposits[9,30] and nonexistent for Archaean rocks. Indeed, the oldest fossil microorganisms reported are filamentous bacteria from Cambrian–Ordovician silica–iron oxide exhalites from northeastern Australia[9]. The discovery of probable microfossils in the Sulphur Springs VMS deposit suggests that a chemotrophic deep-sea hydrothermal biosphere thrived over 3,235 Myr ago, some 2,700 Myr before previously described assemblages[9]. Given the likely abundance of submarine thermal springs on the early Earth[12], it is possible that microbial communities flourished in similar settings well before the Sulphur Springs microorganisms, consistent with proposals for a thermophilic origin of life[7,8,12,13] in deep-sea hydrothermal environments[10,11]. □

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Parasite adaptation to locally common host genotypes

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According to the Red Queen hypothesis—which states that interactions among species (such as hosts and parasites) lead to constant natural selection for adaptation and counter-adaptation—the disproportionate evolutionary success of parasites on common host genotypes leads to correlated selection for sexual reproduction[1–8] and local adaptation by the parasite population[9–14]. Here we determined whether local adaptation is due to disproportionate infection of common host genotypes, and, if so, whether infection of common host genotypes is due to commonness *per se*, or some other aspect of these genotypes. In a reciprocal cross-inoculation experiment parasites occupying the same geographical area (sympatric) infected locally common host genotypes significantly more often than rare host genotypes, whereas parasites occupying separate geographical areas (allopatric) showed no such significant difference. A mixed source of parasites (containing F_1 hybrids) also showed no difference in infection between rare and common host genotypes. These results show that local adaptation results from parasite tracking of locally common host genotypes, and, as such, a necessary condition of the Red Queen hypothesis is met.

The Prosobranch snail, *Potamopyrgus antipodarum*, is widely distributed throughout the freshwater habitats of New Zealand, where populations are composed of either obligately asexual females or mixtures of obligately sexual and obligately asexual individuals[15]. In a study of a clonal population (Lake Poerua, South Island, New Zealand), we found that common clonal genotypes were more susceptible to infection by a digenetic trematode (*Microphallus* sp.) than were rare clonal genotypes[16]. This result is consistent with a theory concerning host–parasite coevolution[1–8]; nevertheless, alternative explanations are possible. For example, suppose that common clones have a greater competitive ability, but a trade-off between competitive ability and resistance to infection renders them more susceptible to parasites. With this model, the best competitors would be most common, but also most susceptible to infection, and this might explain our previous finding that the most common clones were also the most susceptible to infection by the local source of parasites[16]. Here we test the 'trade-off hypothesis' by comparing the susceptibility to infection of rare and common clones when exposed to sympatric, allopatric and hybrid sources of parasites. The trade-off hypothesis would predict that the most common clones from Lake Poerua would be significantly more infected than rare clones, independent of the source of parasites. We contrast this prediction with that of the 'coevolution hypothesis', which predicts that common host genotypes would be more susceptible to only the sympatric source of parasites.

We exposed individuals from two snail populations (Lake Poerua and Lake Ianthe) to two pure sources of parasites (*Microphallus* sp.)

from the same two lakes. We chose the asexual snail population from Lake Poerua because it is composed of multiple clones. We have determined the relative frequency of these clones using allozyme electrophoresis since 1992. We found that between 1992 and 1996 four clones were common (>15%) in one or more years[16]. The remaining fraction of the population (~50% for each year) comprised more than 100 rare clonal genotypes. We chose Lake Ianthe for the allopatric source of parasites. This lake (~80 km south of Lake Poerua) contains a mixed population of sexual and asexual snails[17]. The host genotypes that are common in Lake Poerua are not found in Lake Ianthe, and the two snail populations are genetically differentiated on the basis of allozyme frequency data (Nei's genetic distance equal to 0.121; ref. 17). The parasite populations, however, are not genetically differentiated, also on the basis of allozyme data (Nei's genetic distance equal to 0.011; ref. 17). Finally, we exposed snails from both lakes to a 'mixed' source of parasite eggs by combining adult parasites from both lake populations in the same final host (see Methods). Assuming random mating, roughly half the eggs produced should be hybrids of the two parasite sources.

The specific prediction of the trade-off hypothesis was that common clones from Lake Poerua would be over-infected by parasites drawn from both pure sources (Lake Poerua and Lake Ianthe) and the mixed source. In contrast, the coevolution hypothesis predicts (1) that the pure sources of parasites would be better at infecting snails from their sympatric populations (local adaptation) as a result of tracking locally common hosts, and (2) that common clones in Lake Poerua would be over-infected by only the Lake Poerua source of parasites.

The results were consistent with both predictions of the coevolution hypothesis. Parasites were significantly more infective in sympatric host populations than were allopatric sources of parasites and mixed sources of parasites (local adaptation, Fig. 1). In addition, parasites from Lake Poerua infected common sympatric host clones significantly more than rare sympatric host clones (Fig. 2a). In contrast, allopatric (Lake Ianthe) parasites infected rare clones and common clones from Lake Poerua at statistically indistinguishable rates (Fig. 2b), thereby falsifying the trade-off hypothesis. Similarly, the mixed source of parasites also infected rare and common clones at statistically indistinguishable levels, although infection rates of common clones were slightly lower than rare clones (Fig. 2c). This later result suggests that alleles from Lake Ianthe may have disrupted the specific genetic match between Lake Poerua parasites and the host genotypes that were recently common in Lake Poerua.

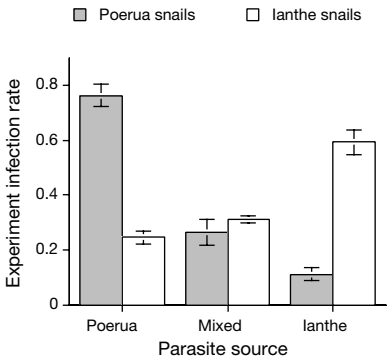

Figure 1 Experimental infection rates of the two snail populations by sympatric, allopatric and mixed parasites. Local parasite adaptation is indicated by significantly higher infection rates for sympatric parasite–host combinations ($\bar{x} = 0.678$; $n = 2$) compared with non-sympatric combinations ($\bar{x} = 0.234$; $n = 4$) (analysis of variance: $F_{1,4} = 28.51$; $P = 0.006$). The mean of four replicates for each treatment combination are given; vertical bars show one standard error of the mean.

In summary, the parasite was found to be adapted to infecting local populations of its snail host, which is consistent with a previous study involving three different lake populations of this same host–parasite combination[13]. In addition, the local adaptation observed here is explained by the greater success of sympatric parasites on locally common host genotypes, which is also consistent with a previous study[16]. Finally, the success of parasites on locally common host genotypes was due to commonness in the strict sense, rather than a correlated phenotypic feature of these common genotypes. This combination of results suggests that local adaptation results from genetically based local coevolutionary interactions as proposed in the Red Queen hypothesis. □

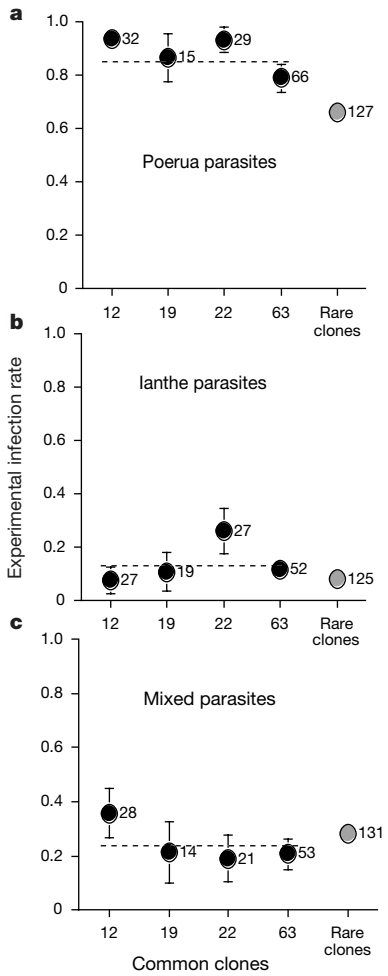

Figure 2 Infection rates of Lake Poerua clones that have been common (12, 19, 22, and 63) and rare between 1992 and 1996 by sympatric, allopatric and mixed parasite sources. Dashed line is the average infection rate of the four common clones. Bars indicate one binomial standard error, and symbol labels give sample size. **a**, Lake Poerua parasites. Common clones were infected at significantly higher rates than rare clones (85.9% and 66.1%, respectively) ($\chi^2 = 14.81$, d.f. = 1, $P < 0.0001$). The four recently common clones were infected at statistically indistinguishable rates ($\chi^2 = 5.935$, d.f. = 3, $P = 0.1148$). **b**, Lake Ianthe parasites. Common clones and rare clones were infected at statistically indistinguishable rates (13.6% and 8.0%, respectively; $\chi^2 = 2.056$, d.f. = 1, $P = 0.1517$). Although the infection rate of clone 22 is slightly higher, the difference in infection rates among the four common clones was not statistically significant ($\chi^2 = 4.267$, d.f. = 3, $P = 0.2341$). When clone 22 is removed, the infection rates of the other three common clones and rare clones are nearly identical (9.5% and 8.0% respectively). **c**, Mixed parasites. Rare clones and common clones were infected at statistically indistinguishable rates (28.2% and 24.1%, respectively; $\chi^2 = 0.537$, d.f. = 1, $P = 0.467$), and the four recently common clones were infected at statistically indistinguishable rates ($\chi^2 = 1.770$, d.f. = 3, $P = 0.6215$).

Methods

Host–parasite system

Potamopyrgus antipodarum serves as the first intermediate host to at least a dozen species of digenetic trematodes. One of these trematode species, *Microphallus* sp., produces encysted larvae (metacercariae) in the snail in 3–4 months under laboratory conditions. The cysts 'hatch' after ingestion by the final host (waterfowl and wading birds), and the resulting hermaphroditic worms produce cross-fertilized eggs within several days; these eggs then pass into the environment. We have found that mice can serve as the final host in laboratory experiments. Snails become exposed to infection after the ingestion of these eggs. An infection resulting from a single egg results in the production of hundreds (or more) asexual larvae within the same snail, thereby sterilizing the host. These larvae then encyst in the snail, but they can be easily removed by dissection.

Experimental infections

Infections of *Potamopyrgus* were carried out in the laboratory (Edward Percival Field Station in Kaikoura, New Zealand) in January 1997 using mice as the final host. Parasite lines were created within 12 laboratory mice by feeding each mouse the metacercarial cysts from 24 infected snails. Four Lake Poerua parasite lines were created using cysts dissected from 24 infected snails collected from the Lake Poerua shoreline; similarly, 4 Lake Ianthe lines were created using cysts from 24 infected snails collected from the Lake Ianthe shoreline. In addition, 4 'mixed' parasite lines were created by combining cysts from 12 infected Lake Poerua snails with 12 infected Lake Ianthe snails. Assuming random mating, 50% of the parasite eggs would be F_1 hybrid genotypes, 25% would be from Poerua × Poerua crosses, and 25% would be from Ianthe × Ianthe crosses. Of the four parasite lines from each parasite source (pure Poerua, pure Ianthe and mixed), two lines were used to infect Lake Poerua snails, and two lines were used to infect Lake Ianthe snails. Parasite eggs were obtained by repeatedly washing the mouse faecal pellets with water. Eggs were collected between two and six days after the mice ingested the cysts.

For each parasite source, we set up 4 replicate containers with 150 snails from the Lake Poerua shoreline and 4 replicate containers with 150 snails from the Lake Ianthe shoreline. Parasite eggs were added to these containers. Snails were kept in the containers with the parasite eggs for 24 days, with water changed twice each day. The snails were then transported to Indiana University where they were held in 4 litres of water. The water was changed regularly and the snails were fed on *Spirulina*. Ninety days after exposure to parasite eggs, we dissected 75 snails from each replicate, and recorded their infection status and the developmental stage of the parasite (early germinal cells lead to blastocercariae, which lead to metacercariae). These stages appear sequentially over a period of about 70–100 days. We limited our analysis to those snails that were infected in the laboratory (that is, early stage infections). We preserved snail tissue samples (head and foot) of Lake Poerua snails for electrophoretic analysis. We used the resulting five-locus allozyme genotypes to identify clonal lineages[15,16]. We further classified these snails as either 1 of 4 recently common clones (clones 12, 19, 22, 63), which accounted for 50% of the sample, or as rare clones, which contained individuals from 89 different clonal lineages.

Infection rate analysis

For results shown in Fig. 1, statistical analysis was conducted using SPSS[18] on untransformed data, where the dependent variable was mean prevalence of infection for the four replicates within a treatment combination (sympatric versus non-sympatric). The homogeneity-of-variance assumption of the analysis was not violated (Bartlett's Box test: $F_{1,23} = 0.145$; $P = 0.706$).

For results shown in Fig. 2, we used a hierarchical log-linear analysis, with replicate, clone identity and infected as factors. For each of the parasite sources, we examined clone-by-infected interaction terms for common clones and rare clones as groups. Significant interactions would indicate that *Microphallus* sources differentially infected rare versus common clones. We also examined clone-by-infected terms for the four common clones individually to see whether they were differentially infected. We report likelihood ratio χ^2 statistics from a backward model selection routine in SPSS[18]. Main and interaction effects involving replicates were non-significant except for the replicate-by-infected term for the mixed source.

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Adhesive force of a single gecko foot-hair

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Geckos are exceptional in their ability to climb rapidly up smooth vertical surfaces[1–3]. Microscopy has shown that a gecko's foot has nearly five hundred thousand keratinous hairs or setae. Each 30–130 μm long seta is only one-tenth the diameter of a human hair and contains hundreds of projections terminating in 0.2–0.5 μm spatula-shaped structures[2,4]. After nearly a century of anatomical description[2,4–6], here we report the first direct measurements of single setal force by using a two-dimensional micro-electro-mechanical systems force sensor[7] and a wire as a force gauge. Measurements revealed that a seta is ten times more effective at adhesion than predicted from maximal estimates on whole animals. Adhesive force values support the hypothesis that individual seta operate by van der Waals forces[8,9]. The gecko's peculiar behaviour of toe uncurling and peeling[2] led us to discover two aspects of setal function which increase their effectiveness. A unique macroscopic orientation and preloading of the seta increased attachment force 600-fold above that of frictional measurements of the material. Suitably orientated setae reduced the forces necessary to peel the toe by simply detaching above a critical angle with the substratum.

The foot of a Tokay gecko (*Gekko gecko*) has about 5,000 setae mm^{-2} (ref. 4) and can produce 10 N of adhesive force with approximately 100 mm^2 of pad area[10] (Fig. 1a–d). Therefore, each seta should produce an average force of 20 μN and an average stress of 0.1 N mm^{-2} (~1 atm). The actual magnitudes could be greater, as it is unlikely that all setae adhere simultaneously. We measured force production by single, isolated seta during attachment using a micromachined, dual-axis, piezoresistive cantilever (Fig. 1e).

To determine how setal force should be measured, we considered