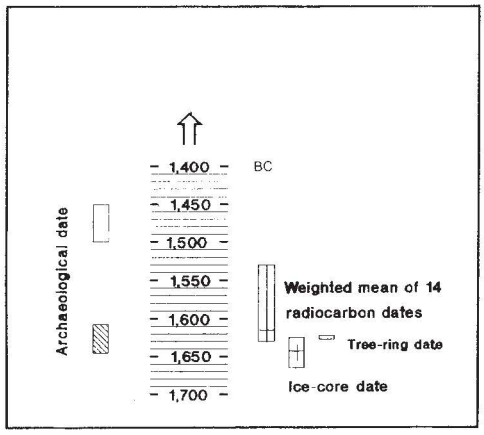

Fig. 4 Dates of the Minoan eruption in calendar years BC obtained by different methods. The open block to the left indicates the traditional archaeological estimate, and the hatched block the revised estimate by Betancourt[15].

particular during the period 1600–2000 BC[27], when the eruption is now thought to have occurred.

The record shown in Fig. 2 indicates a number of acidity peaks superimposed on a general background of acidity in the ice layers. The background oscillates between periods of low general acidity (for example, 1553–1568 BC) and periods with enhanced general acidity (for example, 1431–1441 BC). The enhanced acidity background is largely determined by increased summer melting due to the high summer temperature in south Greenland. The individual acidity peaks superimposed on the background are caused either by acid fallout of volcanic origin or by intense melting during the summer months.

Three methods were used to distinguish between these two types of acidity peaks: (1) visual inspection of the core for distinct melt features, (2) investigation of the annual acidity profiles to separate melt layer acidity (usually irregularly distributed over the year) from volcanic acidity (normally high acidity over the entire annual ice layer) and (3) direct chemical analysis (ion chromatography) of the high-acidity signals. The third method is by far the most powerful and leads to an unambiguous separation, but it is very time consuming. Hence, it was only applied to the three acidity signals, which were considered to be the most likely candidates to be caused by a single and violent volcanic eruption: the peaks at 1428 BC, at 1644 BC and at 1688 BC. The peak at 1428 BC does not represent a particularly high acidity, but it is superimposed on a low-acidity background; the peak at 1644 BC is the highest acidity signal and shows a consistent high acidity over more than a year; the 1688 BC peak is the second highest signal, but is superimposed on a high-acidity background. The results of the chemical analysis of these three events show that the 1644 BC signal is the only one with a high content of sulphuric acid and thus of volcanic origin. The strong increase in the sulphate concentration at 1644 BC is shown in Fig. 3. As the amount of sulphuric acid has already increased at the end of the previous year, the actual eruption probably took place during that year, that is, in 1645 BC. The peaks at 1428 BC and 1688 BC were both dominated by nitric acid. We therefore suggest that the 1644 BC acidity peak is due to the Minoan eruption, and that the date of the eruption is 1645 BC with an estimated standard deviation of ±7 yr, and an estimated error limit of ±20 yr. This suggestion could be further supported, if a corresponding acidity peak of the same age is found in new deep ice cores from central Greenland. In such an ice core major Alaskan explosive eruptions during 1300–1900 BC should also be clearly represented[28]. Dates of the Minoan eruption obtained by different methods, including a tentative date derived from analyses of frost damages in tree rings[29], are summarized in Fig. 4.

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Evidence from a New Zealand snail for the maintenance of sex by parasitism

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The widespread occurrence of sexual reproduction is an important problem in evolutionary theory, because of the cost of producing males in dioecious organisms and the allocation of limited resources in cosexes[1–4]. Here I compare the predictions of the major ecological hypotheses on the maintenance of sex by examining male frequency in *Potamopyrgus antipodarum*, a dioecious freshwater snail with both sexual and parthenogenetic populations[5]. The results do not support the view that sex is maintained by a variable physical environment[6–9], but they are consistent with the idea that sex is favoured by selection resulting from host–parasite interactions[10–14].

Two of the three major ecological hypotheses on the maintenance of sex emphasize variation in the physical environment ('sex' is used here to mean biparental reproduction). The temporal variation hypothesis suggests that sex is favoured by unpredictable environmental changes that occur between generations. This is because sexual populations[6,7], or families[2], would seem more likely to have at least some members capable of survival and reproduction following such changes. The related spatial variation hypothesis[8,9] claims that sex is favoured by intraspecific competition in an environment which is heterogeneous in space, especially if there is a history of competition among sibs[2,15]. This idea is related to models of genetic polymorphism, which show that the maintenance of multiple alleles

is favoured by resource competition in a spatially variable environment[16-18].

The third hypothesis, called the Red Queen hypothesis, emphasizes the importance of frequency-dependent selection resulting from interspecific interactions, such as those between hosts and their parasites[10-14]. The advantage of sex (and recombination[19-20]) under this model is, for the host, the potential for the production of rare offspring that may escape infection and, for the parasite, the capacity to track these genotypes as they become common.

The three hypotheses might apply to *P. antipodarum* as follows. The temporal variation hypothesis predicts that sex should be more common in streams than in lakes, assuming that streams are more unstable in time. This assumption is probably true in general[21], and it has support in the particular case of New Zealand streams[22].

The spatial variation hypothesis, in contrast, predicts that sex should be more common in lakes, making the assumptions that because of their greater stability, intraspecific competition is greater in lakes, and that lakes have multiple niches upon which different snail genotypes might specialize. This same prediction, however, might be arrived at in another way: because stream populations are typically more sparse and individuals are more likely to be isolated by floods, parthenogenesis should be more common in streams (if the probability of isolation is high enough), as it ensures fitness for females in isolation[4,23]. (Note that this idea, called the reproductive assurance hypothesis, is concerned with the loss of sex when there is a risk of isolation. It relies on the other hypotheses for the maintenance of sex when there is no such risk.)

Finally, the Red Queen hypothesis predicts that sex should be most common in populations where there has been a history of parasitism. *P. antipodarum* is the intermediate host for at least fourteen species of digenetic trematodes[24], so assuming that present-day infections are representative of past selection, the Red Queen hypothesis predicts that sex should be positively related to the frequency of trematode-infected snails. Note that the trematodes occur in the snails as larvae, which can not be directly transferred among snails. (Direct transfer from parents to their progeny enhances the expected potential for parasites to maintain sex in their hosts[13].) Most of the larvae go through a second intermediate host (a crustacean), and then mature in a vertebrate. This indirect life cycle means that infection levels are not expected to be a simple function of snail density[25], so that, for example, a dense population could be parasite-free if the final host is absent.

Table 1 Trematode infection of snails from New Zealand streams and lakes

	Streams	Lakes	*H*	*P*
Proportion of males	2.39 (0.86)	12.75 (2.82)	9.708	0.002
Microphallus sp.*	2.22 (0.73)	7.85 (1.88)	12.654	<0.001
Stegodexamene anguillae	0.69 (0.22)	0.73 (0.19)	1.536	0.215
Coitocaecum anaspidis	0.80 (0.41)	0.72 (0.31)	1.568	0.211
Telogaster opisthorchis	0.71 (0.28)	0.72 (0.18)	3.097	0.079
Monostome cercariae (four spp.)	0.46 (0.19)	1.79 (0.82)	6.300	0.012
Xiphidiocercariae (two spp.)	1.81 (0.61)	0.47 (0.21)	1.587	0.208
Total parasites†	7.32 (1.08)	13.89 (2.39)	9.708	0.002

Means with standard error in parentheses for the untransformed percentages of males and individuals infected by the different trematode groups for *P. antipodarum* collected from New Zealand streams ($N = 29$) and lakes ($N = 22$). *H* is the Kruskal–Wallis statistic for a nonparametric, one-way ANOVA on ranked data; *P* is the probability of *H*.

* Undescribed metacercariae tentatively assigned to *Microphallus*; all other species reside in the snail as cercariae.

† Total includes all the listed species plus some rare and unidentified species.

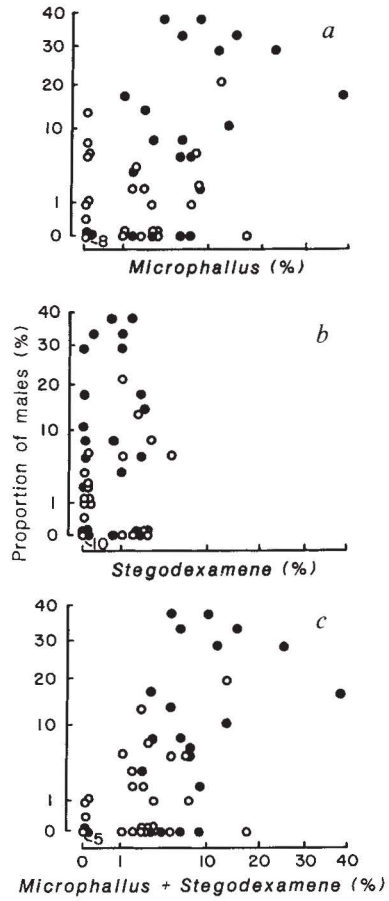

Fig. 1 The proportion of males in stream (○) and lake (●) populations of *Potamopyrgus antipodarum* plotted against the percentages of individuals infected with *Microphallus* sp. (*a*), *Stegodexamene anguillae* (*b*), and either *Microphallus* or *Stegodexamene* (*c*). The axes were back transformed from arcsine $\sqrt{x}$. The lake samples are from lakes Rotorua and Tawawere on New Zealand's North Island and from lakes Forsythe, Ellesmere, Sara, Grasmere, Hawdon, Ianthe, Paringa, Kaniere, Mapourika, Wombat, Wahapo, Brunner, Haupiri, Lady, Poerua, Alexandrina, McGregor, Murray, Ida and Evelyn on the South Island. All stream samples are from streams (mostly unnamed) on the South Island.

To test these hypotheses, *P. antipodarum* were collected from lake margins and in streams throughout New Zealand, particularly on the South Island, and a minimum of forty individuals (usually 100) were sexed and examined for the presence of trematodes under a dissecting microscope (infected individuals rarely contained more than one trematode species). In cases where I sampled the same site more than once, and where Winterbourn[24] sampled two of the same lakes previously, I used the average among samples as the single datum for that site. The frequency of males was used as an estimator of sexual reproduction in each population. (A recent isozyme analysis of *P. antipodarum* confirms that males make a genetic contribution to the offspring of sexual females, and that reproduction in parthenogenetic females is ameiotic[26].)

A significantly higher mean frequency of males was observed in lakes than in streams (Table 1), in direct opposition to the prediction of the temporal variation hypothesis (see also refs 9 and 27). In addition, the average proportion of snails infected by the most common trematode species (tentatively assigned to *Microphallus*) was also greater in lakes. These findings are concordant with the spatial variation and reproductive assurance hypotheses, which both predicted more males in lakes, and the

Table 2 Results of stepwise multiple regression analysis

Step	Source	Regression MS (d.f.)	Residual MS (d.f.)	F	Total R^2
No variables forced					
1	*Microphallus*	0.589 (1)	0.032 (49)	18.56*	0.275
2	*Stegodexamene*	0.589 (2)	0.028 (48)	14.98*	0.384
Habitat forced					
1	Habitat	0.510 (1)	0.033 (49)	15.28*	0.238
2	*Microphallus*	0.369 (2)	0.029 (48)	12.58*	0.344
3	*Stegodexamene*	0.301 (3)	0.026 (47)	11.38*	0.421

Summary table for the stepwise multiple regression of per cent males of *P. antipodarum* against habitat and the trematode groups listed in Table 1. MS, mean square. In the first run, none of the variables were forced[37], and they were entered by the program (SPSS) in order of their unadjusted partial R^2 values until none of the remaining values was significant. In the second run, habitat was forced as the first variable entered, and the remaining values were entered as just described. All continuous variables were transformed (arcsine $\sqrt{x}$) before the analysis.
* $P < 0.001$; all other steps not significant ($P > 0.10$).

Red Queen hypothesis, which predicted a positive relationship between male frequency and infection level.

These hypotheses were compared using a stepwise multiple regression of per cent males (dependent variable) against habitat and the percentages of snails infected by the trematode groups listed in Table 1 (independent variables). The percentage of snails infected with metacercariae of *Microphallus* sp. and cercariae of *Stegodexamene anguillae* entered first and second, respectively; none of the remaining variables were significant. In a second analysis, I forced habitat as the first variable entered, and a similar result was obtained: *Microphallus* entered next, followed by *Stegodexamene* (Table 2). Hence male frequency is significantly correlated with the frequency of infected individuals, even when the effects of habitat are first removed; but the converse is not true. This indicates that parasites are more important than habitat, which supports the Red Queen hypothesis (see also refs 28–30).

The Red Queen hypothesis gains additional support from the relationships between male frequency and infection levels within habitats (Table 3). In lakes, male frequency is significantly correlated with the frequency of snails infected by *Microphallus* (Fig. 1*a*); and in streams, male frequency is significantly correlated with the frequency of snails infected by *Stegodexamene* (Fig. 1*b*). Interestingly, when the frequencies of individuals infected by these two trematodes are added together (Fig. 1*c*), the correlations improve (Table 3).

These results suggest a role for trematodes, especially *Microphallus*, in the maintenance of sex in *P. antipodarum*, but they are not conclusive by themselves. We require further that the correlation between sex ratio and *Microphallus* is not an artefact. One way in which the correlation could be an artefact is if *Microphallus* differentially infects males, creating a situation where the greater the frequency of males, the greater the frequency of infected individuals. To test this idea, I compared the frequencies of males and females infected by *Microphallus* in Lake Alexandrina (chosen because it was my most extensively sampled site). The proportion of males (13 out of 96) infected by *Microphallus* was not significantly different than that for females (83 out of 576): $G = 0.05$, $P > 0.80$. Hence the correlation is probably not an artefact of differential infectivity of the sexes (but it could result from an unknown third force that controls both sex ratio and parasite load).

Table 3 Product-moment correlation coefficients

	Microphallus	*Stegodexamene*	*Microphallus* + *Stegodexamene*
Streams	0.179	0.361*	0.375*
Lakes	0.492*	0.126	0.515*
Streams and lakes	0.524**	0.251	0.583**

Product-moment correlation coefficients for the frequencies of males and the frequencies of *P. antipodarum* infected by *Microphallus* and *Stegodexamene* in New Zealand lakes ($N = 22$) and streams ($N = 29$).
* $P < 0.05$; ** $P < 0.001$.

We also require to know that reproductive success of the snail is negatively affected by trematode infection, and that *P. antipodarum* has a heritable resistance to such infection. It is clear that the trematodes could exert a strong selective force on the snail: following successful infections, the trematodes reproduce asexually and replace most of the viscera and gonad[31] of the snail. This is especially true of *Microphallus*, which encysts in the snail host. It is not presently known whether the snail has a genetically based resistance to infection by the trematodes, but such resistance is known for snails serving as intermediate hosts for schistosomes[32–34]. Also unknown are the proximate determinants of the female-biased sex ratios. Facultative parthenogenesis is one possibility, but it would seem unlikely to account for the sex ratio variation among lakes (unless parthenogenesis is conditional on cues other than the simple presence of males). Another possibility (supported by Wallace[35]) is that sexual females, producing a 1:1 sex ratio, coexist with obligately parthenogenetic females[3] (see also ref. 36). Experiments to test whether parthenogenesis in *P. antipodarum* is faculative or obligate are in progress.

In conclusion, the Red Queen hypothesis is the best supported of the hypotheses considered here, because of the positive correlations between the sex ratio of the snail and infection by trematodes both within and between habitats. This result identifies parasitism, in nature, as a potential source of frequency-dependent selection favoring the maintenance of sex.

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