occurred before, in the geologically recent past (*34*). Gomberg and Ellis (*19*) assumed that events like those of 1811 and 1812 occur about every 1000 years and estimated about 15 to 60 cm of surface uplift per 1000 years (including coseismic uplift and postseismic relaxation). Our results indicate that the LCU block has been rising relative to the Reelfoot Lake block long enough to affect the gradients of some parts of stream networks in the region by at least several meters. Furthermore, as these streams drain recent deposits, uplift has occurred since the time of deposition of the youngest sediments (mid to late Holocene). If each cycle of deformation results in less than 1 m of net uplift, the results of the stream-gradient analysis indicate that more than one cycle has occurred during Holocene time. This also provides evidence that low-order streams adjust their gradients slowly enough for uplift patterns to persist in the landscape record over several thousand years.

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26. The manual data extraction techniques of Merritts and Vincent (*16*) were updated with new software. Furthermore, the multivariate statistical analysis has been replaced with a much more flexible and powerful method of analysis that uses S-Plus language, a high-level statistical programming environment [R. A. Becker, J. M. Chambers, A. R. Wilks, *The New S Language* (Wadsworth and Brooks/Cole, Pacific Grove, CA, 1988); *S-PLUS Reference Manual, Version 3.0* (Statistical Sciences, Seattle, WA, 1991); J. M. Chambers and T. J. Hastie, *Statistical Models in S* (Wadsworth and Brooks/Cole, Pacific Grove, CA, 1992)]. Data collection software works with Macintosh hardware and an Altek AC-40 digitizer; the resolution of the digitizer is 0.001 inches, or 2 feet at the map scale. We constructed a database for all 15 stream segments in the LCU region. The database includes elevations (starting and ending points), lengths, gradients, coordinate positions of upstream and downstream ends of stream segments, and weighted average azimuth orientations for each stream segment.
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Virulence and Local Adaptation of a Horizontally Transmitted Parasite

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Parasites are thought to maximize the number of successfully transmitted offspring by trading off propagule production against host survival. In a horizontally transmitted microparasitic disease in *Daphnia*, a planktonic crustacean, increasing geographic distance between host and parasite origin was found to be correlated with a decrease in spore production and virulence. This finding indicates local adaptation of the parasite, but contradicts the hypothesis that long-standing coevolved parasites are less virulent than novel parasites. Virulence can be explained as the consequence of balancing the positive genetic correlation between host mortality and strain-specific spore production.

Parasites are considered to be a major factor influencing almost every level of organismic evolution (*1*, *2*). Conventional wisdom holds that successful parasite species should evolve to become less virulent over time and therefore that only maladapted novel parasites are harmful (*3*). In contrast, current theory on the evolution of virulence states that pathogenicity can be maintained when it is a direct or indirect consequence of the parasite's exploitation of the host during production of propagules. Therefore, a horizontally transmitted parasite is expected to balance parasite reproduction against host survival, such that parasite transmission is maximized (*4*, *5*).

To understand the processes that influence the evolution of virulence, I studied host fecundity and survival alongside parasite multiplication rate and infectivity in a laboratory transplant experiment. I used host clones of the planktonic crustacean *Daphnia magna* Straus derived from localities up to 3000 km apart and three strains of the horizontally transmitted, cytoplasmic parasite *Pleistophora intestinalis* Chatton [Protozoa, Microsporidia (*6*)] collected from three ponds near Oxford, United Kingdom (Table 1). Horizontal transmission of this parasite occurs when infected hosts pass infective spores with their feces and other hosts capture and ingest the free-floating spores by filter feeding. Vertical transmission does not occur in this microparasite (*7*). Spore-load, here defined as the number of sporophorous vesicles found within the host gut epithelium, increases exponentially over time, which allows estimation of parasite multiplication rate (*7*). The impact

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of the parasite on fecundity, survival, and growth of its clonal host was determined in controlled life-table experiments in the laboratory (8).

Sporeload decreased significantly as a function of geographic distance between host locality and parasite locality, with the highest loads found in the three sympatric host-parasite combinations (Fig. 1A). Geographic distance is used here as a measure of the genetic distance between the novel and original host population, and thus as an estimate for how novel the host is for the parasite (9). Significantly higher sporeloads in sympatric combinations were found even when only the host clones and the parasite strains from the three Oxford ponds were included in the analysis (comparison of sympatric versus novel combinations: $F(1, 8) = 6.80$, $P = 0.035$), indicating divergence of host and parasite populations on a very small geographic scale. Sporeload among novel hosts varied strongly and unpredictably (Fig. 1A), best seen in the variable sporeloads of the three parasite strains in combination with the clones from the Munich population. The mean sporeloads of the parasite strains in the Munich host clones were 0.0, 1.93, and 86.5 ($F_{\text{parasite-strain}} = 29.5$, $P < 0.0001$; $F_{\text{clone}} = 1.49$, $P = 0.25$; $F_{\text{strain} \times \text{clone}} = 3.11$, $P = 0.04$).

The ability of the parasite to infect novel host clones also decreased with distance. The three parasite strains infected all host clones taken from within a 50-km radius of Oxford but did not infect 58% of host clones taken from populations further away. This gradient was also reflected in different measurements of parasite virulence, with geographically distant hosts suffering the least on average (Fig. 1B). However, virulence among novel combinations varied greatly; such combinations produced the highest and the lowest estimates found (Fig. 1B). Among novel host-parasite combinations, both parasite and host genotypes play an essential role in the interaction. Geographic distance explains only a portion of the total variance in host-parasite interactions, and the interaction of novel combinations has a large uncertainty attached to it.

The decrease in sporeload and virulence across distance is not simply the result of reduced infectivity. I repeated the analysis with only those combinations in which the parasite was able to infect its host and found the same decrease across distance (sporeload, $F(1, 13) = 19.19$, $P = 0.001$; mortal-

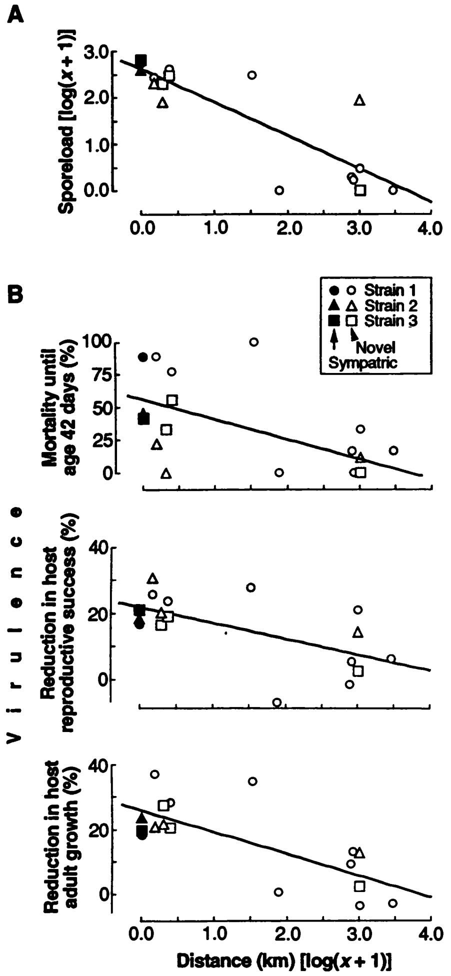

Fig. 1. Means of sporeload (**A**) and virulence (**B**) of all tested host-parasite combinations decrease as a function of geographic distance between parasite and host population origin. Virulence measurements (except mortality) are relative values of the ratios of infected to uninfected hosts [(1 − parasitized female/nonparasitized female) × 100]. Sympatric combinations are assigned to a distance of 0 (filled symbols). Lines indicate simple least square regressions. I tested for parasite strain effects (s) by an analysis of covariance with distance (d) as the covariate. Sporeload: $F_s = 0.73$, $P = 0.5$; $F_d = 33.0$, $P < 0.0001$; $F_{sxd} = 4.73$, $P = 0.03$. Host mortality: $F_s = 5.91$, $P = 0.018$; $F_d = 8.97$, $P = 0.01$; $F_{sxd} = 1.50$, $P = 0.26$. Host reproduction: $F_s = 0.08$, $P = 0.9$; $F_d = 5.25$, $P = 0.04$; $F_{sxd} = 0.16$, $P = 0.8$. Adult growth rate: $F_s = 0.63$, $P = 0.5$; $F_d = 11.1$, $P = 0.007$; $F_{sxd} = 0.75$, $P = 0.5$. The nesting of clones within populations did not reveal significant clone effects; therefore, only population means were used here. To distinguish the symbols of the two North German populations, I shifted the circle for the Lebrader See slightly to the left.

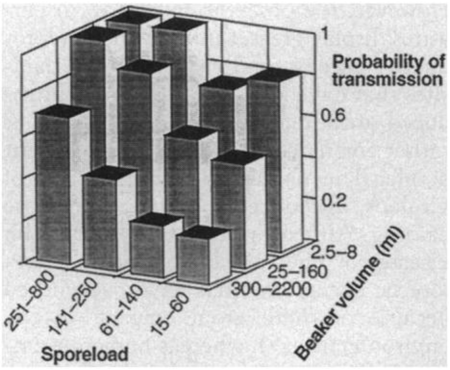

Fig. 2. The probability that an infected female infects an uninfected newborn host with *P. intestinalis* was a function of the beaker size in which both animals were kept together for 2 days and of the sporeload of the infected female. Beaker size is related to the dilution of spores expelled from the infected host and thus relates to host density. For better graphic presentation, I summarized the data in three beaker size classes and four sporeload classes (class size = 6 to 19), because sporeloads were not equally distributed across beaker sizes. A logistic regression showed that sporeload and beaker size had significant effects on the probability of transmission (sporeload: maximum likelihood $\chi^2 = 19.46$, $P < 0.0001$; beaker size: $\chi^2 = 22.15$, $P < 0.0001$, $n = 145$).

Table 1. Combinations of host populations and parasite strains tested experimentally. Host clones were bred from single females isolated in 1992 or in 1993, except for the Munich and Moscow clones, which were raised from sexual eggs collected in December 1992 (17). Parasite strains were obtained from the host population from Oxford ponds 1, 2, and 3 by cloning infected, field-collected, egg-bearing hosts in the laboratory together with their parasites. The parasites were maintained for five to eight host generations in these monoclonal host cultures before the experiment started. The parasite strains do not necessarily represent monoclonal strains. I did not use the host clones in which the parasites were maintained in the laboratory for the transplant experiment. *P. intestinalis* was also found in the Großer Binnensee, Moscow, and Bicester populations. S and N indicate sympatric and novel host-parasite combinations, respectively.

Host origin	Distance from Oxford 1 (km)	Host clones tested (*n*)	Parasite origin in Oxford ponds		
			1	2	3
Oxford 1, south of Oxford	0	3	S	N	N
Oxford 2, south of Oxford	0.5	3	N	S	N
Oxford 3, south of Oxford	1.5	3	N	N	S
Bicester, north of Oxford	40	2	N		
Kew Garden, London	80	2	N		
Grosser Binnensee, North Germany	850	2	N		
Lebrader See, North Germany	850	2	N		
Munich, South Germany	1100	3	N	N	N
Moscow, Russia	3000	2	N		

ity, $F(1, 13) = 7.84$, $P = 0.018$; host reproduction, $F(1, 13) = 2.82$, $P = 0.1$; and adult growth, $F(1, 13) = 8.76$, $P = 0.014$).

High sporeloads indicate high parasite fitness and local adaptation, only if they increase the likelihood of disease transmission. Hosts with high sporeloads were indeed most effective in transmitting the parasite in my experimental situation (Fig. 2) (*10*). The benefits of high sporeloads, however, could be outweighed by parasite-induced host mortality, which would limit the spread of the parasite (*4*, *5*, *11*). In host clones that were tested with all three parasite strains, host mortality was positively correlated with sporeload across these strains [$r = 0.36$, $n = 36$, $P < 0.05$; with clones only from Oxford populations $r = 0.55$, $n = 27$, $P < 0.01$ (*12*)]. This result supports the hypothesis that because of a genetic correlation of parasite reproduction with virulence the degree of virulence of a horizontally transmitted parasite is determined by selection to maximize parasite transmission (*4*).

The theory of the evolution of virulence as outlined above largely ignores host evolution. Selection would favor hosts that minimize their loss in reproductive success by shifting resources from late to early reproduction before the parasite takes its toll (*2*). The three sympatric combinations tested here showed less reduction in reproductive success than did the novel host-parasite combinations with similarly large sporeloads (Fig. 3). This might indicate that these hosts adapted to their local parasite strain by shifting resources from late to early reproduction. This type of fecundity compensation has been suggested for *Daphnia magna* infected with *P. intestinalis* (*7*). Given the high prevalence of this parasite in the three Oxford *Daphnia* populations (*13*), the selection pressure for host adaptation is very strong.

The three *P. intestinalis* strains used here were isolated from three ponds located within 2 km of each other and therefore are likely to be genetically closely related. This factor might affect the general validity of the decline of virulence and sporeload with geographic distance. However, the observation that local parasites display greater infectiveness, reproductive success, and virulence than parasites that have been experimentally introduced into remote host populations is rather common (*14*) and might represent a rule. The numerous recorded cases of virulent, introduced pathogens like those causing African rinderpest, Dutch elm disease, or chestnut blight might therefore be exceptions that have been noted because of their strong impact on the environment (*15*), whereas numerous unsuccessful unmonitored introduced pathogens are likely to have escaped attention (*16*). The occurrence of these virulent exceptions emphasizes the unpredictability of interactions between novel combinations of hosts and parasites, even when we understand the general trends of local adaptation of fast-evolving parasites.

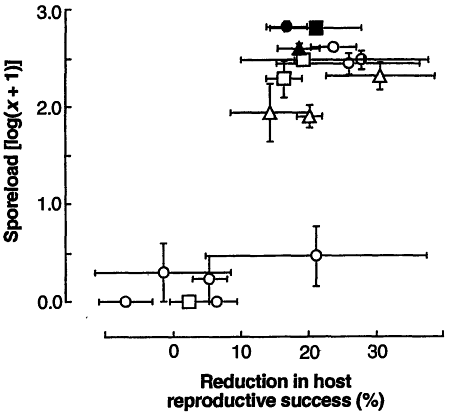

Fig. 3. Sporeload (± SE) in relation to the parasite-induced reduction in host reproductive success. The sympatric combinations (black symbols) cluster in the graph where parasite sporeload is high and reduction of host reproductive success is relatively low in comparison with other combinations with about equally large sporeloads (upper left portion of the cloud of points). Symbols are as in Fig. 1.

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9. The assumption that the host populations are genetically different and that geographic distance estimates genetic distance is reasonable given the low levels of gene flow between *Daphnia* ponds and the large geographic range used here [for example, P. D. N. Hebert, *Hydrobiologia* **145**, 183 (1987); S. Gießler, thesis, Ludwig Maximilians Universität, Munich, Germany (1987)]. Isozyme data from various *D. magna* populations in South England showed strong genetic differentiation even among very closely located ponds [P. D. N. Hebert, *Genetics* **77**, 335 (1974); *Evolution* **28**, 545 (1975)]. For my populations, isozyme data were available only for the Großer Binnensee, Munich, and Moscow populations. These data show significant genetic differences between these populations (D. Ebert and L. Y. Yampolsky, unpublished results).
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13. During the collection of the parasite strains and host clones, the prevalence of *P. intestinalis* was 50 to 90% in the three Oxford ponds and remained high throughout the 1993 summer (D. Ebert, unpublished results).
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