Anciently Asexual Bdelloid Rotifers Escape Lethal Fungal Parasites by Drying Up and Blowing Away
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Anciently Asexual Bdelloid Rotifers Escape Lethal Fungal Parasites by Drying Up and Blowing Away

Christopher G. Wilson* and Paul W. Sherman

Sexual reproduction reduces the efficiency of gene transmission by up to 50%, disrupts favorable gene combinations, spreads disease, and is energetically expensive (1). Yet, paradoxically, sex is nearly ubiquitous: Obligate asexuality occurs in less than 1% of animal species (1, 2), and its scattered distribution at the tips of phylogenetic trees implies that abandoning sex condemns a clade to extinction before it can radiate sufficiently to achieve high taxonomic rank.

The class Bdelloidea (phylum Rotifera) is a famous exception. During three centuries of observation, more than 450 species of these tiny freshwater invertebrates have been described, but neither males nor meiotic eggs have ever been recorded (3). Molecular evidence supports the inference that bdelloid rotifers have been obligately asexual for tens of millions of years (2–5).

Hypotheses for sexual reproduction suggest that it is maintained because it removes deleterious mutations, facilitates coevolution with parasites and pathogens, or both (2, 5–8). However, mutational hypotheses have been challenged empirically (1, 5, 6, 9), and mutational load may be less problematic than predicted, because the bdelloids have persisted despite accumulating mutations faster than related sexual clades (4). In contrast, the coevolution (Red Queen) hypothesis has received considerable empirical and theoretical support (1, 5–11).

Under Red Queen models, biotic interactions favor sex by relentlessly imposing fluctuating, time-lagged, frequency-dependent selection (6–10). However, asexuality can be maintained in one special case: when vulnerable hosts can temporarily shed locally coadapted parasites and pathogens and disperse without them to unaffected habitats (11). Migration and clonal diversity at the population level can then substitute for recombination and genetic diversity at the individual level, allowing mobile hosts to avoid the costs of sex while continuing to “outrun” their enemies (11, 12). Dispersal further favors asexuality by reducing intergenerational transmission of infections (13).

Three unusual characteristics of bdelloid rotifers suggest that this scenario may apply to them (5, 11, 12). First, bdelloids can survive extended (up to 9 years) and repeated bouts of complete desiccation (anhydrobiosis) at any life stage (14, 15). Second, anhydrobiotic bdelloids have an extraordinary potential for wind dispersal as tiny (usually <300 μm) ovoid propagules called “tuns” (14–17), resulting in circumboreal distribution of some taxa (18). Third, bdelloids can thrive in almost any moist habitat, rapidly colonizing even the most ephemeral patches of moss or rainwater on every continent (14–18).

All identified parasites of bdelloid rotifers are oomyctes or hyphomycete fungi. Most belong to Rotiferophthora, a genus of obligate, lethal fungal endoparasites that are exclusive to bdelloids (19, 20). Infections spread when rotifers ingest spores (conidia), which lodge in their pharynx and produce assimilative hyphae. As the rotifer is killed and digested, hyphae puncture its integument and, at the air/water interface, produce conidia that carry hundreds of new conidia.

We investigated whether populations of the bdelloid rotifer Habrobostra elusa can escape the fungal parasite Rotiferophthora angustisporra (19) in space and time, through anhydrobiosis and subsequent wind dispersal. We transferred rotifers from a monoclonal population singly to complete desiccation (anhydrobiosis) at any life stage. In addition, they can temporarily shed locally coadapted parasites and pathogens and disperse without them to unaffected habitats (11). Migration and clonal diversity at the population level can then substitute for recombination and genetic diversity at the individual level, allowing mobile hosts to avoid the costs of sex while continuing to “outrun” their enemies (11, 12). Dispersal further favors asexuality by reducing intergenerational transmission of infections (13).

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References

36. We measured congruence of stratigraphy with phylogeny using the modified Manhattan Stratigraphic Measure (MSM) (37) with the phylogenetic software package TNT (38) and published scripts that allow for uncertainty in first appearance dates for fossil taxa (39).
38. TNT version 1.1; P. A. Goloboff, S. Farris, K. C. Nixon, Materials and Methods www.sciencemag.org/cgi/content/full/327/5965/571/DC1
39. Supporting Online Material www.sciencemag.org/cgi/content/full/327/5965/571/DC1
42. We thank W. Ding and T. Yu for finding the specimen, and the crew of the 2004 Sino-American field expedition for excavating the specimen; H.-J. Wang, X. Ding, and L. Xiang for preparing the fossil; A. Buscalioni, C. Mehleng, and M. Norell for specimen access; and P. Barrett, H. Cameron, J. Conrad, M. Ellison, D. Hone, C. Sullivan, and A. Turner for discussions. Support for this research was provided by the National Science Foundation Division of Earth Sciences and Office of International Science and Engineering of the USA, the National Natural Sciences Foundation of China, and the Chinese Academy of Sciences; and the GRI to the Orcus Foundation, the Hillmar Salree bequest, and the George Washington University.
Conidiophores and exterminating the populations in 18.6 ± 4.0 days (Fig. 1B). Excluding a four-day lag while the fungus regenerated, the time course of the resurgent infection in the rehydrated populations did not differ from that observed in the hydrated, inoculated group (i.e., complete extermination in 14.6 ± 4.0 days versus 13.8 ± 2.6 days; unpaired t test, n = 22, t = 0.544, P = 0.59). Identical fungal regeneration was observed after 14 days of desiccation (with extermination in 14.7 ± 2.3 days).

However, dramatically different results occurred in the other three experimental groups. After 21 days of anhydrobiosis, 60% of rotifer populations remained free of fungal infections for the duration of the experiment (20 weeks). Longer periods of desiccation were even more effective: After 28 and 35 days, 85 and 90.5%, respectively, of rehydrated populations remained fungus-free for the duration of the experiment (20 weeks), indicating that wind dispersal acts in concert with anhydrobiosis to facilitate escape from Rottlerophthora, which is primarily waterborne. Three weeks of in situ desiccation (Fig. 1B) were required to achieve the same rate of parasite elimination (~60%) that was seen after only 7 days in the wind chamber (Fig. 2 and fig. S2). In nature, dispersal distances and maximal durations of anhydrobiosis are certainly far greater (14–18, 20).

Together, our results demonstrate that anhydrobiosis, even for relatively short periods, enables this bdelloid rotifer to disperse without accompaniment by a lethally coadapted fungal parasite.

Although facultative or recently evolved asexuality is common among organisms resistant to physical extremes, as well as those with passively dispersed dormant propagules (1), the extraordinary capabilities of the bdelloids in both regards sets them apart. Few animals or plants can withstand complete loss of cellular water, and even then the ability is usually restricted to proliferate without parasites, whereas six experimental groups were inoculated after 9 days with ~712 (~210 SD) conidia of R. angustispora. The first experimental group remained hydrated throughout the experiment, but the remaining five were desiccated 72 hours after inoculation, maintained at 39.8% relative humidity (~1.8% SD) for 7, 14, 21, 28, and 35 days, respectively, and then rehydrated.

Without anhydrobiosis, R. angustispora exterminated H. elusa populations in 13.8 ± 2.6 days (mean ± SD, n = 12 populations), during which time the uninfected control populations were peaking (Fig. 1A). In the dishes that were rehydrated after 7 days of desiccation, the parasite initially seemed absent. Recovered rotifers were healthy, desiccation had fractured and scattered the fungal conidiophores, and water samples were not infectious to fresh rotifer cultures, suggesting absence of viable conidia (20). However, within 48 hours, hyphae began to re-emerge from the remains of dead rotifers, generating new conidiophores and exterminating the populations in 18.6 ± 4.0 days (Fig. 1B). Excluding a four-day lag while the fungus regenerated, the time course of the resurgent infection in the rehydrated populations did not differ from that observed in the hydrated, inoculated group (i.e., complete extermination in 14.6 ± 4.0 days versus 13.8 ± 2.6 days; unpaired t test, n = 22, t = 0.544, P = 0.59). Identical fungal regeneration was observed after 14 days of desiccation (with extermination in 14.7 ± 2.3 days).

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In nature, desiccated bdelloids are dispersed by wind, adding a second dimension in which they might evade parasites (16). To simulate wind dispersal, we established a heavily infected population of H. elusa in a dish with a natural, friable substrate (sterilized moss and silt) and placed it in a wind chamber with a turbulent flow equivalent to a light breeze (20). Desiccated substrate particles were blown toward empty target dishes 30 to 40 cm away. After 7 days in the chamber, these “wind dispersal” dishes had accumulated 5.01 mg (~2.52 SD) of material; they were then hydrated and monitored for 6 weeks.

Enough rotifers survived to establish populations in 17 of 24 target dishes. Fungal infections appeared in seven of the newly established populations and exterminated them within 16.4 ± 5.0 days (Fig. 2A). However, the 10 remaining wind-dispersed populations (58.8%) never exhibited infections. We replicated this experiment and obtained similar results (i.e., 63.6% of wind-dispersed populations remained fungus-free; see fig. S2). For comparison, “wet dispersal” dishes (n = 24) were created by pipetting 5.0 mg of well-mixed, suspended substrate from an identical infected source dish that was not desiccated (20). Rotifers established populations in all dishes, but fungal conidia also were readily transmitted, and all populations were exterminated in 22.3 ± 5.7 days (Fig. 2B).

Our first experiment indicates that anhydrobiosis allows H. elusa to shed R. angustispora, apparently because the fungus is less resistant to extended desiccation than its host (Fig. 1C and fig. S1). Our second experiment demonstrates that wind dispersal acts in concert with anhydrobiosis to facilitate escape from Rottlerophthora, which is primarily waterborne.
to specific life stages (e.g., seeds, larvae, eggs) (15). Only bdelloid rotifers and certain tardigrades and nematodes can tolerate repeated bouts of desiccation at any life stage (14, 15), and, of these, only the rotifers occur frequently in samples of rain and wind (16). With their smaller, more aerodynamic tails, bdelloids can colonize tiny, isolated microhabitats more rapidly than tardigrades and nematodes (17).

The Bdelloidea have been called an “evolutionary scandal” (2), because their ancient asexuality seemed to challenge all hypotheses for the long-term maintenance of sex. However, if anhydrobiotic dispersal enables bdelloid species to escape temporally and spatially from some or many natural enemies, their coevolutionary burden would be substantially reduced. Therefore, our results are consistent with a scenario in which bdelloids have evaded parasites and pathogens over evolutionary time, without incurring the costs of sexuality, by playing a never-ending game of “hide-and-seek” (11, 12). Decoupling from coevolving enemies could help to explain the ancient asexuality of the Bdelloidea under the broad array of models that derive from or incorporate Red Queen dynamics.

References and Notes

20. See supporting material on Science Online.
21. We thank D. Stottle, G. Masters, and J. Hue for research assistance; K. Hodge, S. Glockling, D. Fontaneto, and G. Barron for helpful advice; U.S. Agricultural Research Service collection of Entomopathogenic Fungi (ARSEF) for fungal isolates; and T. Seeley, J. Scarl, K. Reeve, R. Raguso, C. Lively, N. Hairston, and R. Booker for useful commentaries. Financial support was provided by Sigma Xi, U.S. Department of Agriculture, and Cornell University (Department of Neurobiology and Behavior and an S. H. Weiss Presidential Fellowship to P.W.S.).

Supporting Online Material

www.sciencemag.org/cgi/content/full/327/5965/574/DC1

Materials and Methods

Figs. S1 and S2

References

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Objective Confirmation of Subjective Measures of Human Well-Being: Evidence from the U.S.A.

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A huge research literature, across the behavioral and social sciences, uses information on individuals’ subjective well-being. These are responses to questions—asked by survey interviewers or medical personnel—such as, “How happy do you feel on a scale from 1 to 4?” Yet there is little scientific evidence that such data are meaningful. This study examines a 2005 Behavioral Risk Factor Surveillance System random sample of 1.3 million U.S. citizens. Life satisfaction in each U.S. state is measured. Across America, people’s answers trace out the same pattern of quality of life as previously estimated, from solely nonsubjective data, in one branch of economics (so-called “compensating differentials” neoclassical theory, originally from Adam Smith). There is a state-by-state match (r = 0.6, P < 0.001) between subjective and objective well-being. This result has some potential to help to unify disciplines.

The concept of human well-being is important but difficult to study empirically. One approach is to listen to what human beings say. Research across the fields of psychology, decision science, medical science, economics, and other social sciences draws upon questionnaire data on people’s subjective well-being (1–13). These are numerical scores (e.g., from very satisfied to very dissatisfied) in response to survey questions such as: How happy are you with your life? Sample sizes in these statistical analyses typically vary from a few dozen individuals in a

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