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The curse of the pharaoh hypothesis revisited: Evolutionary coexistence of parasite strains

Several pathogens produce free-living stages that allow the infection to spread from one host to the next indirectly, via an outside environment. Since the reproductive success of pathogens with long-lived spores depends less on the host's survival, it has been hypothesized that such pathogens can afford to exploit their hosts more recklessly and thus evolve higher virulence. We revisit the so called 'curse of the pharaoh' hypothesis and study the evolution of virulence in pathogens that can transmit directly as well as indirectly, via free-living stages. We show that the two transmission routes introduce two environmental feedback variables, which allows for coexistence of two parasite strains one of the two specializes to some extent on direct transmission, while the other makes better use of indirect route of transmission. We give general conditions for coexistence in terms of incidence in host-to-host and host-propagule-host transmission, and discuss the conditions for evolutionary branching leading to coexisting strains in terms of the shape of trade-off functions.