Why does Chytridiomycosis drive some frog populations to extinction and not others? The effects of interspecific variation in host behaviour.

A thesis submitted by

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STATEMENT OF THE CONTRIBUTION OF OTHERS

This thesis was co-supervised by Ross Alford and Lin Schwarzkopf, but also received valuable input from a number of people. Ross Alford contributed in the form of advice on ideas, experimental design, statistical support, editorial assistance, and funded the majority of project costs. Lin Schwarzkopf provided useful comments and editorial assistance on the thesis. Richard Speare, Robert Puschendorf, Robert Jehle, Jérôme Pellet, Lee Skerratt, Andrea Phillott, Bryan Windmiller and Ruth Campbell provided editorial assistance for individual chapters. PCR diagnostic tests for *Batrachochytrium dendrobatidis* were performed by Ruth Campbell at the School of Veterinary and Biomedical Sciences, and Alex Hyatt at the Australian Animal Health Laboratory at CSIRO.

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ABSTRACT

Infectious diseases currently pose a great threat to global biodiversity. One of the most alarming wildlife disease to date is chytridiomycosis, a fatal disease of amphibians caused by the pathogen *Batrachochytrium dendrobatidis.* Chytridiomycosis has been implicated in mass mortalities, population declines, and local and global extinctions of many species of amphibians around the world. However, while some species have been severely affected by the disease, other, sympatric species remain unaffected. One reason why some species decline from chytridiomycosis and others do not may be interspecific differences in behaviour, which may affect the probabilities of acquiring and succumbing to infections. Host behaviour can either facilitate or hinder pathogen transmission, and transmission rates in the field are likely to vary among species according the frequency of factors such as physical contact between frogs, contact with infected water, and contact with environmental substrates that may serve as reservoirs. Similarly, the thermal and hydric environments experienced by frogs can strongly affect their susceptibility to chytridiomycosis, so some interspecific differences in the effects of the disease may also be caused by differences in microenvironment use among species.

I examined the potential effects of behaviour on the susceptibility of different host species to declines caused by chytridiomycosis by tracking three species of stream-breeding frogs in northern Queensland, Australia. The species historically co-occurred at many sites in the Wet Tropics, but high elevation (> 400 m) populations of two species declined to differing degrees in association with outbreaks of chytridiomycosis in recent decades, while low elevation populations remained apparently unaffected. The waterfall frog *Litoria nannotis,* declined to local extinction at all known high elevation sites. All studied populations of the green-eyed tree frog *Litoria genimaculata* at high elevation sites declined to low numbers and then recovered. The third species, the stoney creek frog *Litoria lesueuri,* is not known to have experienced population declines even at high elevations.

I used radio telemetry and harmonic direction finding to track frogs at five sites. Surveys lasted 16 days and were conducted in both the cool/dry season and the warm/wet season. The location of each frog was determined once during the day and once at night over the duration of the survey period. At each location, I recorded contact with other frogs, stream water, and other environmental substrates, its three-dimensional position, movement, habitat type, and body temperature. Retreat sites of *L. lesueuri* and *L. nannotis* were also sampled for *B. dendrobatidis*. Harmonic direction finding obtained fewer fixes on frogs but measures of movement and habitat use did not differ significantly between techniques. In total, 117 frogs were tracked: 28 *L. nannotis,* 27 *L. genimaculata* and 62 *L. lesueuri*. Frequency of contact with other frogs and with water was highest in *L. nannotis,* intermediate in *L. genimaculata*, and lowest in *L. lesueuri.* Environmental substrate use differed among species, and *B. dendrobatidis* was not detected at retreat sites. Movement and habitat use also

differed significantly among species. *Litoria lesueuri* moved more frequently and greater distances and was often located away from streams, moving between intact rainforest and highly disturbed environments. *Litoria genimaculata* moved less frequently and shorter distances, and was more restricted to stream environments, occasionally moved large distances along and between streams, but was never located outside of intact rainforest. *Litoria nannotis* remained in streams during the day, did not move large distances along or move between streams, and was always located within intact rainforest.

In addition to tracking data, I designed, tested, and deployed novel physical models to record the thermal conditions experienced by frogs, regardless of cutaneous resistance to water-loss. These models were placed in species-specific diurnal retreat sites; providing profiles integrated over time of the thermal and hydric regimes of the microenvironments experienced by each species.

Microenvironmental conditions experienced by frogs differed markedly among species and seasons. Retreat sites of the most susceptible species, *L. nannotis*, were almost always within the thermal optimum and never above the thermal tolerance of *B. dendrobatidis*, while retreat sites of the least susceptible species, *L. lesueuri*, were commonly above the thermal optimum and thermal tolerance of *B. dendrobatidis*. Hydric conditions were most suitable for *B. dendrobatidis* growth at *L. nannotis* retreat sites.

Species-specific differences in behaviour are therefore likely to have large implications for the susceptibility of species to decline due to chytridiomycosis. This thesis provides the first empirical confirmation that species-specific differences in behaviour are likely to affect the susceptibility in nature of amphibians to chytridiomycosis. The behaviour of the species most susceptible to *B. dendrobatidis* related declines was the most favourable for the transmission, growth and development of *B. dendrobatidis,* while the behaviour of the species least susceptible to *B. dendrobatidis* related declines had the least favourable for its transmission, growth and development. Species-specific differences in the behaviour of frogs in the field may also explain why infected individuals of some species experience rapid mortality in the laboratory, yet are able to carry infections for extended periods in the field. Temporal and spatial variation in microenvironments available to and used by frogs may also explain variation in infection prevalence and host mortality. Information on amphibian behaviour and microenvironmental use may be useful in evaluating the susceptibility to declines caused by chytridiomycosis in species that presently occur in areas without *B. dendrobatidis.*

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES