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Short communication

Disease dynamics vary spatially and temporally in a North American amphibian

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ABSTRACT

Local environmental conditions are a primary factor influencing chytridiomycosis, an emerging disease caused by the fungus *Batrachochytrium dendrobatidis* (*Bd*) that has affected over 200 amphibian species worldwide. In North America, seasonality and regional habitat differences predict considerable spatial and temporal disease variability, yet the sparse and opportunistic nature of most studies have provided insufficient data for understanding regional *Bd* epidemiology. We present a five-year field study that reveals spatial and temporal *Bd* dynamics across *Lithobates yavapaiensis* populations in Arizona, USA. Two populations showed no *Bd* infection or mortality, ten populations showed winter *Bd* infection, and five populations experienced winter mortality. Infection intensity decreased over winter sampling seasons, whereas mortality and infection prevalence did not change over time. Frogs dying from chytridiomycosis were significantly larger and had significantly higher infection intensities than survivors. We conclude that conserving *L. yavapaiensis* and other native amphibians requires protection and management of riparian ecosystems to promote populations large enough to survive winter cycles of chytridiomycosis.

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1. Introduction

Batrachochytrium dendrobatidis (*Bd*) is a fungal pathogen that has caused declines or extinction in over 200 amphibian species worldwide (Lips et al., 2006; Stuart et al., 2004). The consequences of *Bd* infection vary tremendously with local climatic conditions (Crawford et al., 2010; Kriger and Hero, 2007; Longo et al., 2010). In upland tropical regions that experience little temperature variation across seasons, *Bd* infection often causes rapid declines in host amphibians from epidemics of the skin disease chytridiomycosis (Berger et al., 1998; La Marca et al., 2005). In contrast, amphibians in temperate regions with larger seasonal temperature fluctuations show variable responses to *Bd*, ranging from no observed effects (Garner et al., 2006; Longcore et al., 2007), to sub-lethal fitness costs (Retallick and Miera, 2007), to episodic chytridiomycosis outbreaks and concomitant population declines (Kriger and Hero, 2006; McDonald et al., 2005). These punctuated chytridiomycosis outbreaks usually occur in cool months, suggesting that cooler temperatures promote *Bd* growth, host susceptibility, or both.

With the exception of a few well-studied regions in the Sierra Nevada mountains (Briggs et al., 2010; Vredenburg et al., 2010), studies of local climatic determinants of chytridiomycosis in North

America are patchy and conflicting. One retrospective study of North American museum specimens detected lower *Bd* prevalence in warmer months (Oullet et al., 2005), while a similar contemporary study (Green et al., 2002) found chytridiomycosis outbreaks beginning in warm and cool months. In Canada, *Lithobates pipiens* *Bd* prevalence decreased as mean monthly temperatures increased (Voordouw et al., 2010), but survival did not differ among infected and uninfected individuals. In Mexico, colder temperatures were associated with higher chytridiomycosis severity in four frog species (Hale et al., 2005). In contrast, Lips et al. (2004) documented chytridiomycosis mortalities in upland regions of Mexico during summer. These inconsistent patterns highlight the need to clarify the relationship between *Bd* infection, climate, local environmental conditions, and development of chytridiomycosis in North American amphibians.

Here, we present a five-year field study of *Bd* infection dynamics in the lowland leopard frog (*Lithobates* [*Rana*] *yavapaiensis*), a stream-dwelling species inhabiting southwestern desert regions that has experienced chytridiomycosis die-offs since at least 1992 (Bradley et al., 2002). Documented chytridiomycosis outbreaks in *L. yavapaiensis* occur only in cooler months, but population surveys have been opportunistic (Sredl, 2003). We conducted standardized, repeated surveys of twelve populations and measured *Bd* prevalence, intensity, and mortality in summer and winter. We used these data to determine whether (1) *Bd* infection and mortality vary among populations; (2) *Bd* infection and mortality vary seasonally; (3) *Bd* infection and mortality vary across

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years; and (4) *Bd* infection intensity, prevalence, and mortality co-vary within and across seasons, years and populations. Finally, we exploited the unique thermal dynamics in one region of Arizona to directly evaluate the relationship between water temperature, *Bd* infection, and chytridiomycosis.

2. Methods

We surveyed twelve *L. yavapaiensis* population localities in Arizona, USA, in summer (July–August) and winter (January–February) from 2006 to 2010 (Fig. S1). All populations were surveyed within three weeks to limit within-season variation due to local environmental conditions. We gave equal survey time and effort across seasons, years, and localities, and used diurnal visual encounter surveys (Crump and Scott, 1994) to measure the abundance of adult and sub-adult *L. yavapaiensis* individuals. We toe-clipped and swabbed the epidermis of each individual using sterile fine-tip swabs (Medical Wire & Equipment Co. MW113) following standardized protocols (Hyatt et al., 2007). Frogs were handled with unused latex gloves to prevent pathogen transmission. Recapture rates were low (mean = 0.4%), thus we treated each sampling season as independent.

We used a Taylor 9842 temperature logger to record water temperatures. Within each locality, we took three mid-afternoon readings and retained the maximum recorded temperature. We separated Muleshoe Ranch (MR) into three sub-regions based on mean temperature variation across microhabitats: (1) MR_{HS} is a thermal spring >50 °C at the source and >30 °C throughout the frog sampling region, (2) MR_{SS} is a pond 0.5 km away fed by a thermal spring >30 °C at the source and 20–30 °C throughout the frog sampling region, and (3) MR_{BC} is a canyon stream 1.4 km away that has average winter water temperatures of 10 °C. To evaluate the role of water temperature, we separated frog populations into thermal spring localities (MR_{HS} and MR_{SS}) and non-thermal spring localities (all other populations).

Eight of our 12 localities are Nature Conservancy properties with continual monitoring since the 1980s by on-site staff (MR_{SS}, MR_{HS}, MR_{BC}, AC, HR), or sites that have been surveyed by Tucson Herpetological Society volunteers since the 1990s (AS, TV, CIC; Table S1). For each dead and dying frog, we recorded the date of death as the first date that our team, a volunteer, or a site manager observed the mortality event. We collected individuals with signs of chytridiomycosis (i.e., skin redness, lethargy, failure to seek cover, and loss of righting ability) for overnight observation; if death occurred within 24 h and the individual tested positive for *Bd*, we categorized these frogs as chytridiomycosis mortalities. Individuals found dead during winter without other apparent causes of death (i.e., predation or injury) and testing positive for *Bd* were also considered chytridiomycosis mortalities.

We extracted DNA from swabs using PrepMan Ultra (Applied Biosystems; Hyatt et al., 2007). Infection prevalence and intensity were determined using quantitative PCR (Boyle et al., 2004). Infection intensity was measured as the number of zoospore equivalents per swab, and individuals were considered *Bd*-positive at ≥ 1 zoospore equivalents. Values were not obtained for the January 2007 season. We calculated *Bd* infection as the number of positives divided by the total number of frogs swabbed and *Bd* mortality as the number of dead frogs divided by the total number of frogs observed. We calculated 95% Clopper–Pearson binomial confidence intervals from observed proportions of infection and mortality. We compared *Bd* infection, chytridiomycosis mortality, numbers of frogs, and water temperatures using two-tailed paired sample Wilcoxon signed-rank tests and rank sum tests. We compared *Bd* infection intensity among dead, dying and asymptomatic individuals using two-tailed Student's *t*-tests assuming unequal variances.

3. Results

We sampled 692 *L. yavapaiensis* individuals from 12 localities in Arizona, USA, with a mean pairwise population distance of 198 km (Table S1). No mortality and low *Bd* prevalence (1.6%) occurred in summer. In contrast, all populations were infected with *Bd* in winter except for House Spring (HS) and Aliso Spring (AS; Fig. 1A), populations separated by 265 km. Of the ten infected populations, five experienced winter mortalities, and observed levels of *Bd* infection and mortality varied among localities (Fig. 1A). *Bd* infection ($P = 0.005$) and mortality ($P = 0.02$) were significantly lower in summer compared to winter. *Bd* infection was significantly higher than mortality in summer ($P = 0.03$) and winter ($P = 0.008$).

Winter *Bd* infection prevalence did not significantly change across sampling years, nor did winter *Bd* mortality (Fig. 1B). In contrast, infection intensity significantly decreased from 2008 to 2010 ($P = 0.02$; Fig. 1C). Across all years, *Bd* infection intensity limits were 0–4040 zoospore equivalents among the 139 individuals sampled in winter months. Notably, we detected little *Bd* on individuals found dead; mean infection intensity was 1280.6 for dying individuals, 276.3 for healthy individuals, and 15.6 for individuals found dead. Dead individuals laid out for a mean of 5.3 days (range: 0–16) without predation before we collected them. Individuals found alive but showing signs of chytridiomycosis all died within 24 h, and these moribund individuals had significantly higher mean infection intensity compared to individuals found dead ($P = 0.02$). Individuals sampled from populations with compared to without mortality did not differ in mean infection intensity ($P = 0.89$). Among individuals sampled in winter, mean body mass was significantly higher for dead (28.5 g) and dying (33.7 g) individuals compared to asymptomatic individuals (18.2 g; $P = 0.01$). *Bd* infection prevalence was highly seasonal, increasing in winter and decreasing in summer for all populations across the five-year sampling period (Fig. 2A). Across all localities, the mean number of frogs observed was significantly higher in summers compared to winters ($P = 0.001$). At Tanque Verde Canyon (TV), the locality with the highest infection and mortality prevalence (Fig. 1A), we did not observe any frogs after summer 2009.

We examined the effect of water temperature on *Bd* infection and chytridiomycosis mortality by comparing thermal springs to other localities. Among non-thermal spring localities, maximum water temperature was significantly higher in summer versus winter ($P = 0.002$), whereas maximum water temperature at thermal springs did not differ significantly in summer versus winter ($P = 0.18$; Fig. 2B). In summer, maximum water temperature was not significantly different at thermal versus non-thermal spring sites ($P = 0.166$). In contrast, maximum winter water temperature was significantly higher at thermal versus non-thermal spring sites ($P = 0.03$; Fig. 2B). Concordantly, chytridiomycosis mortality was significantly higher at non-thermal versus thermal spring localities in winter ($P = 0.05$). However, *Bd* infection did not differ significantly at non-thermal spring versus thermal spring localities in winter ($P = 0.28$) or summer ($P = 0.39$).

4. Discussion

Seasonal and spatial variation in disease prevalence are common in human and wildlife systems (Hosseini et al., 2004; Pascual and Dobson, 2005) and can arise from numerous factors, such as pathogen thermal requirements (Van Riper et al., 1986), host immunity changes over seasons or temperatures (Cheng et al., 2009), and variable host population genetic diversity (Pearman and Garner, 2005). However, *Bd* modeling suggests that intraspecific variation in infection outcomes do not require differences in susceptibility, virulence, or environment, but can instead result

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