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POPULATION ECOLOGY - ORIGINAL RESEARCH

Infection dynamics in frog populations with different histories of decline caused by a deadly disease

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Abstract Pathogens can drive host population dynamics. Chytridiomycosis is a fungal disease of amphibians that is caused by the fungus *Batrachochytrium dendrobatidis* (*Bd*). This pathogen has caused declines and extinctions in some host species whereas other host species coexist with *Bd* without suffering declines. In the early 1990s, *Bd* extirpated populations of the endangered common mistfrog, *Litoria rheocola*, at high-elevation sites, while populations of the species persisted at low-elevation sites. Today, populations have reappeared at many high-elevation sites where they presently co-exist with the fungus. We conducted a capture–mark–recapture (CMR) study of six populations of *L. rheocola* over 1 year, at high and low elevations. We used multistate CMR models to determine which factors (*Bd* infection status, site type, and season) influenced rates of frog survival, recapture, infection, and recovery from infection. We observed *Bd*-induced mortality of individual frogs, but did not find any significant effect of *Bd* infection on the survival rate of *L. rheocola* at the population level. Survival and recapture rates depended on site type and season. Infection rate was highest in winter when temperatures were favourable for pathogen growth, and differed among site types. The recovery rate was high (75.7–85.8 %) across seasons, and did not differ among site types. The coexistence of *L. rheocola* with *Bd* suggests that (1) frog populations are becoming resistant to the fungus, (2) *Bd* may have evolved lower virulence, or (3) current environmental conditions may be inhibiting outbreaks of the fatal disease.

Keywords Coexistence · Disease dynamics · Fungus · Host–pathogen interactions · Infectious disease

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Introduction

Pathogens can reduce host density and, in some cases, drive their host populations to extinction (McCallum and Dobson 1995; Tompkins and Begon 1999; De Castro and Bolker 2005; Jolles et al. 2006). Paradoxically, many populations suffering from a variety of infectious diseases are relatively stable (Albon et al. 2002; Caley et al. 2002; Krkosek et al. 2011; Tobler et al. 2012). Disease-induced mortality causes host population declines only if it is additive to other sources of host mortality (i.e. competition or predation; Anderson and May 1979; Burnham and Anderson 1984; Tompkins et al. 2002; Jolles et al. 2006). In contrast, when mortality is compensatory, increases in disease-induced deaths are balanced by a reduction in natural mortality from other causes (Tompkins and Begon 1999; Lebreton 2005; Jolles et al. 2006), and populations will remain stable. The distinction between additive and compensatory mortality effects of pathogens is important to conservation biologists because it describes the difference between declining and stable populations (e.g. Kistner and Belovsky

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2014). Capture–mark–recapture (CMR) surveys combined with recent advances in multi-state models have greatly improved our ability to study the effects of pathogens on wildlife populations (Faustino et al. 2004; Conn and Cooch 2008). The great advantage of these multi-state models is that they allow wildlife biologists to model the processes of infection and recovery in addition to estimating the effect of the pathogen on host survival and host detection (recapture). As a result, these multi-state models have been used to study a wide variety of wildlife diseases (Retallick et al. 2004; Lachish et al. 2007, 2011a, b; Chambert et al. 2012; Voordouw et al. 2015).

Pathogens are believed to play an increasingly important role in the endangerment and extinction of their host species (Smith et al. 2006). The mode of transmission plays a critical role in whether or not pathogens can drive their host populations to extinction (Begon et al. 2002; McCallum et al. 2001; Potapov et al. 2012). Pathogens with density-dependent transmission cannot reduce their host populations below a critical minimum size (Nokes 1992). In contrast, pathogens that have frequency-dependent transmission (Potapov et al. 2012), or that can persist in another host species or the abiotic environment, are more likely to cause extinction. For example, transmission of the parapoxvirus from the introduced grey squirrel to the native red squirrel is eliminating the latter from the UK (Tompkins et al. 2002). Similarly, the introduction of a pathogenic trematode by the European black rat caused the extinction of the endemic Christmas Island rat within 5 years (Wyatt et al. 2008). Pathogen-mediated extinction can also occur between different stages of the same host population. For example, tadpoles can act as asymptomatic reservoir hosts for a fungal pathogen that kills adult frogs (Rachowicz et al. 2006).

Chytridiomycosis is caused by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*), and has contributed to declines and extinctions of amphibian populations on most continents (Berger et al. 1998; Daszak et al. 1999, 2003). Severe *Bd* infections disrupt cutaneous function, causing an imbalance in electrolyte transport across the epidermis, which leads to asystolic cardiac arrest (Voyles et al. 2009). Chytridiomycosis can cause extinctions because *Bd* has a broad host range, including both larval and adult amphibians, some of which are resistant to its effects and act as reservoirs for the pathogen (Brunner et al. 2004; Retallick et al. 2004; Lips et al. 2006; Murray et al. 2009; Sapsford 2012). The presence of reservoirs for the fungal pathogen greatly increases the potential for extinction from disease.

The host–pathogen dynamics underlying chytridiomycosis are strongly influenced by temperature (Woodhams et al. 2003; Piotrowski et al. 2004; McDonald et al. 2005; Rodder et al. 2008; Kinney et al. 2011; Savage et al. 2011; Stevenson et al. 2013, 2014). In the laboratory, *Bd* grows optimally from 15 to 25 °C and dies above 28–30 °C (Piotrowski et al. 2004; Stevenson et al. 2013). In the wild, *Bd* prevalence is often higher in cooler seasons and lower in warmer ones (Woodhams and Alford 2005; Brem and Lips 2008; Voordouw et al. 2010; Whitfield et al. 2012; Sapsford et al. 2013). *Bd* is more prevalent at higher elevations, presumably because temperatures are cooler (Woodhams and Alford 2005; Brem and Lips 2008; Pullen et al. 2010; Sapsford et al. 2013). Temperature may influence susceptibility to infection and disease-induced mortality. Individuals that maintain higher body temperatures have a lower risk of infection by *Bd* (Rowley and Alford 2013). Apparent extinctions are more common at high elevations (Richards et al. 1993; McDonald and Alford 1999) and warmer sites can serve as climatic refugia for vulnerable species (Puschendorf et al. 2009, 2011). In addition, water flow may transport *Bd* zoospores from upland to lowland areas and thereby increase the prevalence of *Bd* infection in lowland areas, even though they tend to be warmer and less conducive to *Bd* growth (Sapsford et al. 2013).

Many amphibian populations infected with *Bd* do not decline or go extinct. Some species appear to always coexist with the pathogen, while others do so only in certain circumstances (Briggs et al. 2005; Alford 2010; Kilpatrick et al. 2010). For example, populations of the Australian hylid frog *Litoria wilcoxii* have a high prevalence of *Bd* but infection has no negative effect on adult survival in this species (Kriger and Hero 2006). In other species, however, survival of infected individuals can be lower than uninfected individuals (Murray et al. 2009; Longo and Burrowes 2010; Pilliod et al. 2010). Thus, the effects of infection by *Bd* are species-specific, and there are some species in which the host–pathogen relationship has apparently changed. A few species have reappeared following apparent local extirpations (Retallick et al. 2004; McDonald et al. 2005; Rodriguez-Contreras et al. 2008; Newell et al. 2013). In the mid-1980s, the Eungella torrent frog (*Taudactylus eungellensis*) suffered *Bd*-related population declines; however, 10 years later, infected and uninfected individuals had similar survival rates (Retallick et al. 2004). Recovery from population extirpation has rarely been studied in the amphibian–*Bd* system. In particular, the rate of survival, of acquiring *Bd* infection, and of recovering from *Bd* infection have never been compared among multiple populations of the same species with different histories of decline. However, such comparisons may be highly informative for understanding how virulence can undergo rapid shifts in host–pathogen relationships.

We examined the effects of *Bd* infection on natural populations of the common mistfrog (*Litoria rheocola*). In the early 1990s, during outbreaks of chytridiomycosis, *L. rheocola* declined and disappeared at all surveyed sites

above approximately 400 m elevation in the Australian Wet Tropics, while persisting, apparently without declining, at sites below that elevation (Richards et al. 1993; McDonald and Alford 1999). Approximately 19 years after declines at high elevations were documented, *L. rheocola* had reappeared at some sites above 400 m (McDonald et al. 2005). A recent study on populations of *L. rheocola* at two lowland sites where *Bd* was present but where declines had not occurred found no significant effect of *Bd* infection on survival (Phillott et al. 2013). The present study is novel because we compared the virulence of *Bd* between populations of *L. rheocola* that were recently extirpated by disease to those that apparently never declined due to disease outbreaks. We conducted a 1-year-long CMR survey in six *L. rheocola* populations that differed in their history of *Bd*-related extirpation and recolonization. We used multistate modelling of our CMR data to estimate the effect of *Bd* on the survival of *L. rheocola*, and to estimate the rate that frogs would acquire and recover from their *Bd* infections.

Materials and methods

Study species

The common mistfrog, *Litoria rheocola*, is a small, endangered, hylid frog (IUCN Red List 2012) that occurs near rocky, fast-flowing, rainforest streams in northern Queensland, Australia (Hoskin and Hero 2008; Dennis 2012). At night and on rainy days, males typically perch on rocks, logs, and streamside vegetation near riffles (Hoskin and Hero 2008; Dennis 2012), and on dry days, they typically shelter between moist rocks in the stream bed (Roznik and Alford 2015). Females are elusive as they only visit the streams briefly to breed (Phillott et al. 2013; S. Sapsford, unpublished data).

Study sites

Our six study sites were in the Wet Tropics Bioregion in northern Queensland, and included two replicates for each of three site types. High-elevation sites were higher than 400 m ASL (McDonald and Alford 1999) and had populations of *L. rheocola* prior to 1990, which had disappeared by 1994 (McDonald and Alford 1999), but had reappeared after 2001 and before the start of the present study (R. Alford, personal observation). These two sites, Bobbin Bobbin Falls (17°22′43″S, 145°46′21″E; 700 m ASL) and Windin Creek (17°22′04″S, 145°42′52″E; 718 m ASL), are both in Wooroonooran National Park. The creek bed at Bobbin Bobbin Falls had large boulders with sections of smaller rocks, whereas the bed of Windin Creek consisted primarily of small rocks (1–10 cm in diameter). Both creeks were 3–4 m wide. At low-elevation sites (<400 m ASL), populations of *L. rheocola* did not suffer any apparent declines (McDonald and Alford 1999). We examined two types of low-elevation sites: non-contiguous low-elevation sites (which had no connection to high-elevation sites) and contiguous low-elevations sites that were connected to high-elevation sites by stream flow. Contiguous sites received an inflow of cooler water from high elevations, had lower water temperatures and could receive *Bd* zoospores drifting downstream from higher elevations (Brittain and Eikeland 1988). These circumstances could alter the prevalence and dynamics of *Bd* infections (Sapsford et al. 2013). Our contiguous low-elevation sites and our high-elevation sites were not connected, as they were in separate watersheds. The two contiguous low-elevation sites were Frenchman Creek (17°18′29″S, 145°55′16″E; 59 m ASL) in Wooroonooran National Park and Tully Creek (17°46′29″S, 145°38′38″E; 114 m ASL) in Tully Gorge National Park. The beds of these creeks consisted of large boulders with sections of smaller rocks (1–10 cm in diameter). Frenchman creek was 10 m wide and Tully Creek was 3–4 m wide. Our two non-contiguous low-elevation sites were Mena Creek (17°38′59″S, 145°59′13″E; 59 m ASL) located on private land and Stoney Creek (17°55′17″S, 146°4′7″E; 18 m ASL), in Hull River National Park. The beds of both these creeks consisted primarily of small rocks (1–10 cm in diameter). Both creeks were 3–4 m wide. All our creeks had areas differing in flow rates (0.05–2 m/s), depending on whether the area was a pool, run or riffle. All creeks were covered with a canopy of rainforest trees and the understory vegetation included vines, ferns, and palms.

Field methods

We sampled adult frogs on five different occasions: austral winter (June–July 2010), spring (October 2010), summer (January 2011), autumn (March–April 2011), and the following winter (June–July 2011). Each of these five occasions was planned to include five consecutive nights of capture–mark–recapture sampling at each site. Sixteen of the planned 150 sampling nights were not carried out because sites were flooded for extensive periods. Adult frogs were located at night using visual and auditory cues, and were captured using a clean plastic sandwich bag worn as a glove. Captured frogs were swabbed to detect *Bd,* measured to the nearest 0.1 mm (snout–urostyle length), weighed to the nearest 0.1 g, and marked with visible implant elastomer (VIE) as detailed below. To prevent disease transmission among frogs, a new pair of powder-free latex gloves was used to handle each individual. After processing, frogs were released at their capture location.

Assessing infection status

Frogs were swabbed using a sterile, fine-tip, dry rayon swab (#113, Dry swabs; Medical Wire and Equipment, Corsham, Wiltshire, UK). The ventral side of each foot, inner thigh area, both lateral sides of the stomach, medial section of the stomach, and ventral side of each hand were swabbed three times, because the fungus is mainly found on these areas of the body (North and Alford 2008; Skerratt et al. 2008). Swabs were placed in separate, labelled vials and refrigerated immediately following collection. In the laboratory, swab samples were tested for *Bd* infection using real-time quantitative PCR (Boyle et al. 2004). Samples were run in triplicate and considered positive for *Bd* if the number of zoospore equivalents was greater than zero in at least two of the three PCR reactions. It is normal practice to consider all frogs that test positive for *Bd* (as defined by Hyatt et al. 2007) as being infected (e.g. Skerratt et al. 2008; Murray et al. 2009; Phillott et al. 2013). As *Bd* can occur in the environment, it is theoretically possible to recover *Bd* from the skin of an animal that is not infected. However, we consider such environmental contamination unlikely in the present study.

Marking technique

Each individual was marked using visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, WA, USA). Five colours of VIE were used to create a marking scheme: pink, orange, yellow, green, and blue. VIE was injected subcutaneously into the inner thigh of the frog (Schmidt and Schwarzkopf 2010; Sapsford et al. 2014, 2015) using a 29-gauge insulin needle (Terumo Medical, Elkton, MD, USA). Individual frogs received up to three marks in total, with marks placed in the left leg, the right leg, or both (Sapsford et al. 2015). Needles were reused and were sterilized by placing them in 70 % ethanol for at least 20 s (Johnson et al. 2003; Department of Environment and Heritage 2006).

Multi-state capture–mark–recapture statistical analysis

We considered data from male *Litoria rheocola* only ($n = 1340$ individuals) because relatively few females were captured ($n = 110$ individuals). Our capture histories included information on a dynamic state variable: the *Bd* infection status of each frog at every capture. We therefore used multi-state CMR models to analyse the effect of infection status on the survival rate (monthly) and the recapture rate per sampling occasion. In addition, multi-state models can estimate the transition rates between states. In our study, these transition rates refer to the monthly infection rate (the rate of acquiring a new infection) and to the monthly recovery rate (the rate of losing an existing infection). An infection event occurred when a healthy individual became infected between sampling periods (i.e. a transition from *Bd*-negative to *Bd*-positive status) whereas a recovery event occurred when an infected individual cleared its infection (i.e. a transition from *Bd*-positive to *Bd*-negative status). The infection and recovery rates are critical epidemiological parameters for understanding the dynamics of infectious diseases.

We used program MARK (White and Burnham 1999) to analyse our data, examining a set of models created using a priori hypotheses. These hypotheses concerned the effects of four explanatory variables: infection status (2 levels: uninfected or infected by *Bd*), population sampled (6 levels: one each of the six populations), site type (3 levels: high elevation, contiguous low elevation, and non-contiguous low elevation), and season (4 levels: winter, spring, summer, autumn). As the factor 'site type' was a reduced form of the factor 'population', these two fixed factors were never included in the same model. For the recapture parameter only, we included an additional covariate, the number of sampling nights per sampling trip (1–5), to account for differences in capture effort, because some populations were not sampled all five nights because of temporary flooding caused by heavy rainfall.

We had an a priori expectation that season, population or site type, and possibly their interactions, would influence the survival and recapture rates, as previous work on other frog populations has demonstrated such effects (Longo and Burrowes 2010; Sapsford et al. 2013). We also wanted to test whether *Bd* infection influenced the survival and recapture rates of *L. rheocola*, as it can in other species (e.g. Murray et al. 2009). We hypothesized that the recapture rate would be a function of the sampling effort (number of nights spent sampling on each sampling occasion), and we therefore included the covariate of sampling effort in the models of the recapture rate.

We started with a model in which each of the four population parameters was a function of site type, season, and their interaction (model 30 in Table S5). We first simplified the models for infection and recovery while keeping the models for survival and recapture constant. Once we had found the best models for infection and recovery, we simplified the models for survival and recapture. In this way, we found a group of models that best captured the variation in the CMR data using the explanatory factors of season and site type. We then added *Bd* infection status to the survival and recapture models and sampling effort to the recapture models to examine whether these factors improved the model fit. We also ran a series of models that used the fixed factor 'population' rather than the fixed factor 'site type'.

We derived an estimate of lack of fit for the best model in our candidate set using the median $\hat{c}$ approach (White and Burnham 1999). To quantify the amount of over-dispersion, we calculated the value of the variance inflation factor ($\hat{c}$). The model fit the data well ($\hat{c} = 1.19$), so no adjustment for over-dispersed data was necessary. We used Akaike's Information Criterion corrected for small sample size (AICc) to guide model selection (Burnham and Anderson 2002). In the AICc model selection paradigm, models with lower AICc values are considered more parsimonious explanations of the data than models with higher AICc values. In the present study, we do not present a single best model. Instead, we present the top 15 models and, for each of the four CMR parameters (survival, recapture, infection, and recovery), we note how often a given explanatory factor occurred. We also calculated the weight or support for each model by using the differences in AIC_C values between the top model and the other models in the candidate set (Burnham and Anderson 2002). We calculated model-averaged parameter estimates (and their 95 % confidence limits) to incorporate model uncertainty in our estimates of the survival, recapture, infection, and recovery rates (Burnham and Anderson 2002). The means of two groups were considered different if the 95 % confidence limits (CL) of one group did not overlap the mean of the other group and vice versa.

Results

Of the 1340 marked males we analysed, 275 were recaptured at least once. We observed 36 infection events (transition from *Bd*-negative to *Bd*-positive status) and 53 recovery events (transition from *Bd*-positive to *Bd*-negative status). We used month (30 days) as the unit of time in our MARK analysis. The survival rate therefore refers to the probability that a frog survived for 1 month. The infection rate is the probability that an uninfected frog acquires the *Bd* infection after having survived the previous month. The recovery rate is the probability that an infected frog clears the *Bd* infection after having survived the previous month. The recapture rate is the probability that a previously marked frog is captured over the duration of the sampling occasion (in our case, 5 days) conditional on the assumptions that the frog is alive and present in the area during this time.

There was no obvious best model in our MARK analysis (Table 1) as the top five models were all within 2 ΔAICc units of each other (Burnham and Anderson 2002). The top 15 models combined had 98.1 % of the support (Table 1). The remaining 53 models had a combined support of 1.9 % and therefore made a negligible contribution to the model-averaged parameter estimates. We discuss the factors that

Table 1 Multi-state capture–mark–recapture (CMR) models of *Bd* infection in the common mistfrog, *Litoria rheocola*

Model ID	Model	AICc	Delta AICc	AICc weight	Model likelihood	Num. par.	Deviance
1	S(SE)R(EF + ST)T1(ST*SE)T2(SE)	2093.0	0.0	0.175	1.000	24	283.0
2	S(ST*SE)R(EF + ST)T1(ST*SE)T2(SE)	2093.4	0.4	0.140	0.800	32	266.9
3	S(SE)R(EF + ST)T1(ST*SE)T2(.)	2093.5	0.5	0.135	0.771	21	289.7
4	S(ST*SE)R(EF + ST)T1(ST*SE)T2(.)	2093.9	0.9	0.111	0.638	29	273.6
5	S(SE)R(EF + ST)T1(ST + SE)T2(.)	2094.9	1.9	0.066	0.378	15	303.5
6	S(ST*SE)R(ST)T1(ST*SE)T2(SE)	2095.0	2.1	0.062	0.357	31	270.6
7	S(ST*SE)R(EF + ST)T1(ST + SE)T2(.)	2095.2	2.2	0.058	0.333	23	287.3
8	S(ST + SE)R(EF + ST)T1(ST*SE)T2(SE)	2095.3	2.4	0.054	0.307	26	281.3
9	S(SE)R(EF + ST)T1(ST + SE)T2(SE)	2095.7	2.7	0.045	0.257	18	298.1
10	S(ST*SE)R(EF + ST)T1(ST + SE)T2(SE)	2096.0	3.0	0.038	0.220	26	281.9
11	S(SE)R(EF + ST)T1(SE)T2(.)	2096.7	3.7	0.028	0.159	13	309.3
12	S(ST*SE)R(EF + ST)T1(SE)T2(.)	2096.9	3.9	0.025	0.143	21	293.1
13	S(ST*SE)R(EF + ST)T1(SE)T2(SE)	2096.9	4.0	0.024	0.138	24	287.0
14	S(ST*SE)R(ST)T1(SE)T2(.)	2098.5	5.5	0.011	0.063	20	296.8
15	S(ST + SE)R(EF + ST)T1(SE)T2(.)	2099.0	6.0	0.009	0.050	15	307.5

The top 15 candidate models with the lowest corrected Akaike information criterion (AICc) are shown. The multi-state CMR recapture histories had two states: uninfected or infected with *Bd*. There are four CMR variables: the survival rate (*S*), the recapture rate (*R*), the infection rate (*T1*), and the recovery rate (*T2*). The explanatory factors include: site type (*ST*), season (*SE*), and sampling effort (*EF*). The explanatory factors population and *Bd* infection status did not occur in any of the top 15 models. Shown for each model are: the *AICc* value, the difference in AICc from the top model (*Delta AICc*), the AICc weight or support, the model likelihood, the number of parameters (*Num. Par.*), and the deviance

Model notation follows the conventions used by R where a colon (:) indicates an interaction and an asterisk (*) indicates the main effects and all possible interactions

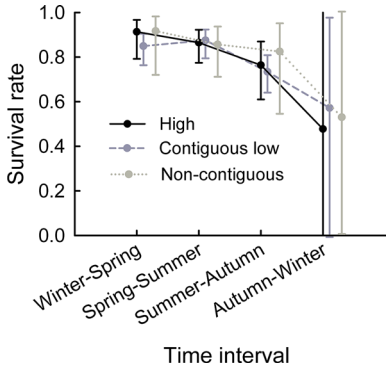

Fig. 1 Monthly survival rate in populations of the common mistfrog (*Litoria rheocola*) in northern Queensland, Australia. Monthly survival was estimated for each of the 12 combinations of site type (high elevation, contiguous low elevation, and non-contiguous low elevation) and season (winter–spring, spring–summer, summer–autumn and autumn–winter). The parameter estimates were model-averaged over the set of 68 multi-state capture–mark–recapture models. *Vertical bars* 95 % confidence limits of the mean

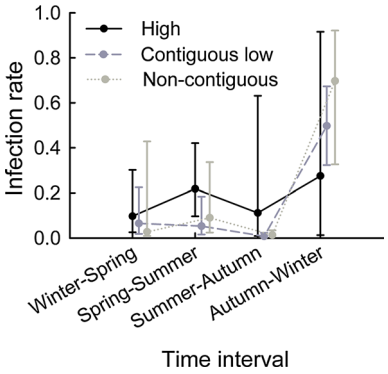

Fig. 2 The monthly infection rate of *Bd* infections in populations of the common mistfrog (*Litoria rheocola*) in northern Queensland, Australia. Monthly infection rate was estimated for each of the 12 combinations of site type (high elevation, contiguous low elevation, and non-contiguous low elevation) and season (winter–spring, spring–summer, summer–autumn and autumn–winter). The parameter estimates were model-averaged over the set of 68 multi-state capture–mark–recapture models. *Vertical bars* 95 % confidence limits of the mean

contributed to variation in the top 15 models under appropriate subheadings below.

Survival rate

In general, the model selection results indicated that the survival rate depended on season (15 of the top 15 survival models included season; cumulative support = 98.1 %; Table 1). There was less support that the survival rate depended on site type (10 of the top 15 survival models included site type; cumulative support = 60.9 %; Table 1). The survival rate was high for the winter–spring and spring–summer seasons at all site types (85.1–91.3 %), slightly lower for the summer–autumn season (75.2–85.1 %), and lowest for the autumn–winter season (47.7–59.0 %; Fig. 1; Table S1). However, the large 95 % CL precluded inferences regarding the autumn–winter survival estimate (Fig. 1). Models that treated survival and/or recapture as a function of *Bd* infection status had low support (all weights <0.01; Table 1; Table S5). Thus, infection by *Bd* had no discernable effect on the survival or recapture rates in these *L. rheocola* populations.

Infection rate

There was strong support that the infection rate depended on season (15 of the top 15 infection models included season; cumulative support = 98.1 %; Table 1) and moderately strong support that the infection rate depended on site type (10 of the top 15 infection models included site type; cumulative support = 88.4 %; Table 1). Infection was lower at both low-elevation site types (range 0.3–8.0 %) than the high-elevation sites (9.7–21.8 %) for the first three seasons (Fig. 2). In the last season (autumn–winter), the infection rate at both low-elevation site types was higher (49.3–68.8 %) than the high-elevation sites (27.5 %; Fig. 2; Table S2).

Recovery rate

There was moderate support that the recovery rate depended on season (7 of the top 15 recovery models included season; cumulative support = 53.8 %; Table 1) and no support that the recovery rate depended on site type (0 of the top 15 recovery models included site type; cumulative support = 0.0 %; Table 1). The recovery rate

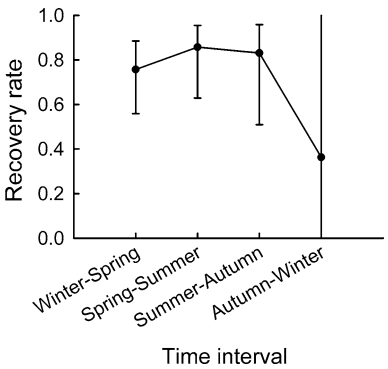

Fig. 3 The monthly recovery rate from *Bd* in populations of the common mistfrog (*Litoria rheocola*) in northern Queensland, Australia. Monthly recovery rate was estimated for each of the four seasons (winter–spring, spring–summer, summer–autumn and autumn–winter) and there was no effect of site type. The parameter estimates were model-averaged over the set of 68 multi-state capture–mark–recapture models. *Vertical bars* 95 % confidence limits of the mean

was high for the first three seasons (75.7–85.8 %) then decreased for the autumn–winter season (36.3 %), although the large 95 % CL preclude inferences regarding this season (Fig. 3; Table S3).

Recapture rate

There was strong support that the recapture rate depended on site type (15 of the top 15 recapture models included site type; cumulative support = 98.1 %; Table 1). There was also strong support that the recapture rate increased with greater sampling effort (13 of the top 15 recapture models included sampling effort; cumulative support = 90.8 %; Table 1). There was no support that the recapture rate depended on season (0 of the top 15 recapture models included season; cumulative support = 0.0 %; Table 1). The recapture rate was usually highest at the high-elevation sites (range for first three capture occasions: 29.4–60.4 %), intermediate at contiguous low-elevation sites (32.7–38.8 %), and lowest at the non-contiguous low-elevation sites (15.0–18.7 %; Fig. 4; Table S4). As with the other parameters, the low precision of the recapture rate for the last sampling occasion prevents us from making inferences about this capture occasion.

Discussion

Survival rate

We found no negative effects of *Bd* infection on the survival of *L. rheocola* (Table 1) despite the fact that our study included upland populations that had drastically declined due to *Bd* outbreaks in the past. Our results were consistent with another recent study on two lowland populations of *L. rheocola* that were from the same area (the Australian Wet Tropics bioregion) as those in the present study (Phillott et al. 2013). That study also found no significant effect of *Bd* infection on the survival of *L. rheocola* (Phillott et al. 2013). Studies on some amphibian–*Bd* systems have reported similar results: surveyors have observed chytridiomycosis-induced mortality in the field but subsequent CMR studies have found no evidence that *Bd* infection reduced frog survival (Retallick et al. 2004; Voordouw et al. 2010). In contrast, studies on other species have found the expected negative effects of *Bd* infection on frog survival (Murray et al. 2009; Longo and Burrowes 2010; Pilliod et al. 2010).

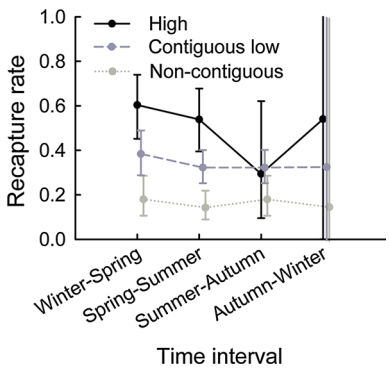

Fig. 4 Recapture rate in populations of the common mistfrog (*Litoria rheocola*) in northern Queensland, Australia. Recapture rate was estimated for each of the 12 combinations of site type (high elevation, contiguous low elevation, and non-contiguous low elevation) and season (winter–spring, spring–summer, summer–autumn and autumn–winter). The parameter estimates were model-averaged over the set of 68 multi-state capture–mark–recapture models. *Vertical bars* 95 % confidence limits of the mean

The lack of a negative effect of *Bd* on the population-level survival of *L. rheocola* seems paradoxical because some individual frogs *are* killed by chytridiomycosis at lowland sites in the Wet Tropics (Woodhams and Alford 2005; Phillott et al. 2013). In the present study, we observed 18 individuals with symptoms of chytridiomycosis (i.e. sloughing skin, loss of righting reflex, lethargy), of which 15 tested positive for *Bd*. Frogs displaying such symptoms usually die from the disease (Voyles et al. 2009). The apparent paradox that some *L. rheocola* die from chytridiomycosis but that *Bd* has no effect on frog survival at the population level could simply reflect relatively high variances and low differences in mortality rates between infected and uninfected individuals. However, if chytridiomycosis-induced mortality was additive to other sources of mortality, all populations of *L. rheocola* should have declined since the outbreak of *Bd*. Upland populations of *L. rheocola* did suffer drastic and abrupt *Bd*-associated declines in the early 1990s, and all populations at high-elevation sites were extirpated (Richards et al. 1993; McDonald and Alford 1999). Since then, some high-elevation populations of *L. rheocola* have reappeared (Woodhams and Alford 2005; S.J. Sapsford, personal observation), and low-elevation populations have persisted, relatively stably, in association with the pathogen (McDonald and Alford 1999; Phillott et al. 2013).

The recovery and relatively long-term coexistence of *L. rheocola* populations with *Bd* implies that mortality is compensatory at the population level. Compensatory mortality occurs when an increase in mortality from one source, for example infection by pathogens, is compensated for by a decrease in mortality from other sources, so that the host population remains stable (Tompkins and Begon 1999; Lebreton 2005; Jolles et al. 2006). Compensatory mortality could occur if predators remove diseased individuals instead of healthy ones or if chytridiomycosis-induced mortality reduces the intensity of intra-specific competition for resources within the frog population. Compensatory

mortality may occur in all amphibian species that coexist with *Bd* and where infected individuals have higher mortality rates (Murray et al. 2009; Longo and Burrowes 2010; Pilliod et al. 2010). In Switzerland, for example, *Bd*-infected populations of the endangered midwife toad, *Alytes obstetricians*, remained stable and did not have lower population growth rates than uninfected populations (Tobler et al. 2012), even though chytridiomycosis produced mortality in some individuals. Our study therefore suggests that the nature of chytridiomycosis-induced mortality in the upland populations of *L. rheocola* must have switched from additive to compensatory since the declines that followed the initial appearance of *Bd* in these populations. Numerous explanations have been suggested for such switches, including the evolution of immune defences or the skin microbiome (Woodhams et al. 2007) and changes in thermoregulatory behaviour (Rowley and Alford 2013).

We found that season was the most important explanatory factor for variation in survival. The monthly survival rate for the first three seasons was 75 % or greater (Fig. 1; Table S1), suggesting that overwintering frogs have relatively high survival into and through the summer reproductive season. Survival may decrease during the autumn–winter season but the low precision of the autumn–winter estimate prevents us from being certain of this. Our model selection results suggested that site type and the site type by season interaction had a weak effect on survival.

Infection and recovery rates

Relatively few studies have quantified the infection rate of *Bd* infections in frog populations (Olson et al. 2013). Murray et al. (2009) found high infection (5–60 % per month) in a single population of the cascade treefrog, *Litoria pearsoniana*. In contrast, the infection rate in our *L. rheocola* populations was low for the winter–spring, spring–summer, and summer–autumn seasons across all site types (0.3–21.8 % per month), then increased substantially for the autumn–winter season (27.5–68.8 % per month; Fig. 2; Table S2). Seasonal variation in the infection rate was likely related to seasonal variation in temperature. During the summer, temperatures were frequently above 25 °C (Sapsford et al. 2013), which slows *Bd* growth (Stevenson et al. 2013), and temperatures were sometimes above 30 °C (1.2 % of recorded temperatures; Sapsford et al. 2013), which kills *Bd* (Longcore et al. 1999; Piotrowski et al. 2004; Stevenson et al. 2013). In contrast, during the winter, temperatures were frequently between 17 and 23 °C (Sapsford et al. 2013), which is within the optimal growth range of *Bd* (Piotrowski et al. 2004; Stevenson et al. 2013). The infection rate was also affected by differences among site types (Table 1). Infection was generally higher at the cooler high-elevation sites (Fig. 2; Table S2), which may promote *Bd* growth and transmission compared to the low-elevation sites (Retallick 2002; Woodhams and Alford 2005; Brem and Lips 2008; Pullen et al. 2010; Sapsford et al. 2013). Variation in the infection rate may also be driven by differences among sites in the microhabitat use and movement patterns of frogs (Rowley and Alford 2007; Roznik and Alford 2015).

The high recovery rate in our populations of *L. rheocola* probably facilitates their coexistence with *Bd*. The recovery rate in our study (36.3–85.8 % per month) was equal or greater to that found in other species. For example, the recovery rate in a population of the cascade treefrog, *Litoria pearsoniana*, was 30–60 % per month over a 5-month period (Murray et al. 2009). A study on the Stoney Creek frog, *Litoria wilcoxii*, found only 7 recovery events out of 26 recaptures (26.9 %) over several months (Kriger and Hero 2006). A study on the northern leopard frog, *Rana pipiens*, recorded 3 recovery events out of 31 recaptures (9.7 %; Voordouw et al. 2010). The last two studies did not use multi-state CMR methods and so the recovery rate was not expressed relative to a time unit.

The lack of strong effects of season and site type on the recovery rate (Fig. 3; Table 1; Table S3) suggests that, in our study, this variable was relatively independent of environmental conditions. Recovery may depend more strongly on the frog immune system (Woodhams et al. 2010), on frog thermoregulatory behaviour (Rowley and Alford 2013; Roznik and Alford 2015), or on changes in the virulence of *Bd* (Phillips and Puschendorf 2013). There is growing evidence that antimicrobial peptides (Woodhams et al. 2007, 2010) and skin microbiota (Bell 2012) can inhibit *Bd* and that these immune responses may become more effective after epidemics. We previously reported seasonal differences in the prevalence of *Bd* infections across the three site types (Sapsford et al. 2013). The present study shows that this seasonal variation in *Bd* prevalence is driven by variation in the infection rate and not the recovery rate, as the former, and not the latter, was strongly affected by site type and season.

Recapture rate

We found that recapture rate was strongly affected by site type, but was not affected by season or *Bd* infection status (Fig. 4; Table S4). Similarly, there was no evidence that *Bd* infection status influenced the recapture rate in a population of *L. pearsoniana* (Murray et al. 2009) or in two lowland populations of *L. rheocola* (Phillott et al. 2013). This result suggests that our observed estimates of *Bd* prevalence were not biased by differences in recapture rate between infected and uninfected animals (Faustino et al. 2004).

We recaptured relatively low proportions of individuals at the non-contiguous low-elevation sites (55 recaptured out

of 498 marked = 11.0 %) compared to the contiguous low-elevation (141 recaptured out of 629 marked = 22.4 %) and high-elevation sites (73 recaptured out of 213 marked = 34.3 %). The recapture rate is reduced when animals are not present in the sampling site at the time of sampling. Frogs, being ectotherms, may be more likely to move further and more frequently in the warmer lowland sites than the cooler highland sites (e.g. Schwarzkopf and Alford 2002). Thus, one possible explanation is that low-elevation frogs were more likely to move away from the sampling zone surrounding the creek than the high-elevation frogs. Another explanation is that the availability of water at the landscape level was lower at the lowland sites, thus attracting frogs from a greater area. Changes in the regional availability of water at the landscape scale can influence the number frogs around water bodies, such that, when there is more water at the landscape scale, the density of frogs around any particular water body decreases, because frogs can use alternative aquatic habitats (Alford and Richards 1999; Schwarzkopf and Alford 2002).

Factors facilitating coexistence

Our results of high survival, low infection, and high recovery provide evidence that common mist frogs are coexisting with the pathogen *Bd*. There are a number of possible mechanisms for coexistence, some of them quite complex. We suggest two possible explanations why coexistence may occur in our frog populations. First, the recovery rate was much higher than the infection rate, which reduced the prevalence of the disease, and thus the frequency of disease-induced mortality. Recovery rate may have increased since initial epidemic outbreaks of chytridiomycosis because frogs have evolved behavioural or immune-related defences against *Bd*. Some declining frog populations appear to lack antimicrobial peptides that protect against *Bd* (Woodhams et al. 2006; Conlon et al. 2013). In *L. serrata*, lowland populations coexisting with *Bd* have more effective anti-microbial peptide defences than highland populations, which have higher variability in peptide expression (Woodhams et al. 2010). *Litoria rheocola* do have antimicrobial peptides, but little is known about their effectiveness against *Bd*. In addition, *L. rheocola* are hosts to environmental bacteria that play a role in inhibiting the growth of *Bd* (Bell 2012). Alternatively, coexistence may have developed because *Bd* has evolved lower virulence (Ebert and Hamilton 1996; Phillips and Puschendorf 2013).

A second explanation is that changing environmental conditions may influence disease-induced mortality in the host. For example, destruction of the canopy cover by tropical cyclones may lower the risk of *Bd* infection in rainforest frogs (Roznik et al. 2015) perhaps because of reduced shade and increased environmental temperatures (Terrell et al. 2014). Our study sites were damaged by cyclone Yasi in 2011, but damage was patchy, and air temperatures have been relatively constant since the early 2000s (Bureau of Meteorology 2012) when frog populations reinvaded our study sites. This observation suggests that environmental change did not contribute to the reduction in *Bd*-induced population declines in *L. rheocola*.

Unravelling the ecological and evolutionary factors influencing the coexistence of pathogens and hosts is complicated. The comparative method is a powerful approach for unravelling this complexity. By comparing replicate populations of a host species, we can identify the factors that influence the dynamics of infectious diseases. Such knowledge is critical for protecting vulnerable animal populations from disease epidemics. Across an environmental gradient that strongly affects the dynamics of *Bd* infections (Sapsford et al. 2013), we have shown that *Bd* has no negative effect on the survival of *L. rheocola* at the population level; that differences in *Bd* prevalence among populations appear to be driven by differences in infection rather than recovery; and that future CMR studies should consider that recapture rates can differ among high- and low-elevation sites. Our demonstration that variation in *Bd* prevalence is driven by differences in infection rate will allow future studies to elucidate the mechanisms responsible for population recovery and host–pathogen coexistence in this system. Understanding these mechanisms will provide general insight into host–pathogen ecology.

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Author contribution statement SJS, RAA, and LS conceived and designed the methodology. SJS performed the fieldwork. SJS and MJV analysed the capture–mark–recapture data using multi-state models. SJS, MJV, RAA, and LS wrote the manuscript.

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