Chytridiomycosis and Seasonal Mortality of Tropical Stream-Associated Frogs Fifteen Years after Introduction of *Batrachochytrium dendrobatidis*

Running head: Seasonal mortality in chytridiomycosis

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ABSTRACT

Assessing the effects of diseases on wildlife populations can be difficult in the absence of observed mortalities, but it is crucial for threat assessment and conservation. We performed an intensive capture-mark-recapture study across seasons and years to investigate the effect of chytridiomycosis on demographics in 2 populations of the threatened common mist frog (*Litoria rheocola*) in the lowland wet tropics of Queensland, Australia. Infection prevalence was the best predictor for apparent survival probability in adult males and varied widely with season (0-65%). Infection prevalence was highest in winter months when monthly survival probabilities were low (approximately 70%). Populations at both sites exhibited very low annual survival probabilities (12-15%) but high recruitment (71-91%), which resulted in population growth rates that fluctuated seasonally. Our results suggest that even in the absence of observed mortalities and continued declines, and despite host-pathogen co-existence for multiple host generations over almost 2 decades, chytridiomycosis continues to have substantial seasonally fluctuating population-level effects on amphibian survival, which necessitates increased recruitment for population persistence. Similarly infected populations may thus be under continued threat from chytridiomycosis which may render them vulnerable to other threatening processes, particularly those affecting recruitment success.

INTRODUCTION

It is crucial to understand the effect of endemic disease (disease constantly present in a region; Porta et al. 2008) on wildlife populations for threat assessment and conservation but this is difficult to achieve in the absence of mass mortalities and census information (Wobeser 2007). Endemic disease can have insidious effects on population persistence because it can cause slow declines, suppress population densities, or render populations more vulnerable to stochastic events and other threatening processes (e.g., gradual decline of the southern corroboree frog [*Pseudophryne corroboree*] [Hunter et al. 2010]). Subtle individual-level effects of endemic disease can range from decreased reproduction to morbidity and mortalities that may be unobservable due to their sporadic occurrence and acute course; increased predation of morbid individuals; rapid carcass decomposition, and scavenging (Stallknecht 2007). Difficulties detecting population-level effects may be compounded where compensatory mechanisms confound effects on population growth rates, such as where increased recruitment compensates for reduced survival (Muths et al. 2011).

The recently emerged global pandemic of chytridiomycosis, a fungal skin disease of amphibians (*Batrachochytrium dendrobatidis*, hereafter Bd), has caused the decline and extinction of approximately 200 species of frogs worldwide (Skerratt et al. 2007). *Batrachochytrium dendrobatidis* has now become endemic in many climatically suitable environments around the world (Fisher et al. 2009; Kinney et al. 2011; Murray et al. 2011). Although much research has focused on overt epidemics or disease-induced declines in critically endangered species, there are potentially many more species globally that continue to be threatened by endemic chytridiomycosis. It is crucial to understand the population-level effect of endemic diseases such as chytridiomycosis so that populations at greatest risk of future collapse can be identified.

To better understand the nature of population effects of endemic chytridiomycosis, we performed an intensive capture-mark-recapture (CMR) study in 2 endemically infected populations of the common mist frog (*Litoria rheocola*) in the lowland wet tropics of northeast Queensland, Australia. The common mist frog is a suitable model for investigating endemic chytridiomycosis because individuals are susceptible to Bd and active in streams throughout the year, and they share habitat with at least 6 other species of obligate stream-associated frogs that similarly have undergone severe population declines in Queensland since 1985 (McDonald & Alford 1999). Populations of the common mist frog disappeared from upland protected areas (>400 m asl) from 1989-1994, but they persisted in anecdotally stable populations at lower elevations (Richards et al. 1993; McDonald & Alford 1999). These declines were due to the arrival of Bd, which has been detected in frogs collected from the region since 1989 (Murray et al. 2010a). We sought to assess the overall effect of endemic chytridiomycosis on populations approximately 15 years after introduction.

Results of previous empirical studies suggest that due to thermal tolerance limits of Bd, infection prevalence in common mist frogs should vary seasonally (McDonald et al. 2005; Forrest & Schlaepfer 2011). In addition, endemic infection may continue to cause individual frog mortality, as demonstrated by Murray et al. (2009) in southeast Queensland 30 years after disease emergence. On the basis of these results, we hypothesize that overall survival probabilities vary seasonally in our populations, where lowest survival correlates with highest prevalence and occurs during winter months. This scenario does not elucidate the effect of endemic chytridiomycosis on populations however, for which it is necessary to understand population responses to putatively lowered survival rates of infected individuals. Such populations may persist and appear stable over the long term if overall population abundance is reduced, if infection prevalence is very low, if other regulatory mechanisms compensate for chytridiomycosis-induced mortalities (e.g., predation mostly of sick individuals), or if mechanisms for compensating recruitment are invoked. Alternatively, consistent with the finding of recent upland recolonization, 15 years of co-evolution at our study sites may have altered the host-pathogen interaction and led to the expression of effective innate immunity or reduced pathogen virulence (McDonald et al. 2005). This second scenario implies a declining effect of chytridiomycosis on the population and favors long-term persistence through survival of reproductive adults.

We investigated whether in a long-term endemically infected tropical system Bd may still have an important seasonal effect on overall apparent survival probabilities at the population level.

METHODS

Species ecology and Study Sites

The common mist frog is a nocturnal rainforest and wet sclerophyll forest specialist with an obligate association to creeks and streams for breeding. Males are present throughout the year and exhibit territorial intermale spacing along stream banks or rocks, whereas females are present from March-July (McDonald & Alford 1999; Hodgkison & Hero 2002). Females and juveniles spend less time along the stream; likely, they favor terrestrial foraging sites (Hodgkison & Hero 2002).

From November 2005 to October 2007 we surveyed a 150-m-long transect of an unnamed creek in lowland wet tropical rainforest of Tully Gorge National Park (hereafter Tully) (145°38'E 17°46'S, 130 m asl) for a total of 26 sampling trips. Each sampling trip to Tully consisted of 1-3 consecutive sampling nights. The interval between trips averaged 28 days (range 6-88). Similarly, a transect 200 m in length along the creek from Bridge 7 in Murray Upper National

Park (hereafter Kirrama) (145°52'E 18°11'S, 206 m asl) was surveyed during 18 sampling trips that consisted of 1-4 sampling nights. The interval between trips averaged 31 days (range 9 to 139). We selected study sites and transect lengths in accordance with breaks in habitat to minimize expected frog migration out of the site (a large waterfall and the Tully River bounded the Tully site) and for logistical reasons. Both populations could migrate relatively freely through the rainforest to adjacent streams, however dispersal lessened during the drier winter months, and frogs were rarely encountered in the Tully River downstream of the Tully site.

The creek beds at the 2 sites were composed of granite rocks of variable size; water flow was generally fast in the wet summer months and there were small waterfalls and riffles (>5 cm/second^2). Slower-flowing connected pools formed in winter when rainfall decreased. Surrounding vegetation was characterized by mesophyll to notophyll vine forest on moderately fertile granite and rhyolite that had patches of remnant vegetation including pink bloodwood (*Corymbia intermedia*) and red stringybark (*Eucalyptus pellita*) (DERM 2011).

Tully Gorge and Murray Upper National Parks are in the monsoonal Austral tropics and have warm, moist summers with high rainfall from December to March. Spatially interpolated weather values were obtained from the SILO climate database (Jeffrey et al. 2001). At Tully average maximum temperature and rainfall for summer over the study period were 31.6 °C and 1066 mm respectively, and for winter were 24.7 °C and 220 mm. At Kirrama average maximum temperature and rainfall for summer were 28.1 °C and 712 mm respectively, and for winter were 20.2 °C and 148 mm (BOM 2008).

Mark-recapture sampling

Frogs were observed after dusk with spotlights and captured by hand by experienced workers. Workers wore a new pair of plastic gloves for each frog they caught (Phillott et al. 2010b). Snout-urostyle length (SUL) was measured with Vernier calipers, and clinical signs of disease were recorded if observed (peripheral erythema and skin shedding). Gender and breeding characteristics were also recorded (Hodgkison & Hero 2002).

We examined adult frogs for previous identifying toe-tip marks or missing digits. If not previously marked, we made a unique toe-tip mark by removing the toe-disc of up to 5 digits with disinfected dissection scissors (Phillott et al. 2007; Phillott et al. 2010a). The toe-tipping scheme has been used with the Tully population since 1992 (McDonald et al. 2005). Juvenile frogs (<24 mm SUL) were not marked and were excluded from analyses.

We swabbed each frog caught with a sterile dry swab following standard protocols (Hyatt et al. 2007). Swabs were stored dry at 4 °C and were analyzed within 6 months of collection for the presence of Bd DNA with the TaqMan real-time PCR protocol (Hyatt et al. 2007). Individual swabs were analyzed in triplicate, and each run included an internal positive control. A single positive result of one zoospore equivalent (ZSE) or greater was considered positive for optimized sensitivity (Murray et al. 2009; Skerratt et al. 2011).

Capture-Mark-Recapture modeling

We sought to quantify unbiased estimates of demographic parameters in combination with infection data to explore the population-level effect of endemic chytridiomycosis. Hence, we used capture-mark-recapture (CMR) (Cooch et al. 2012; Lindberg 2012) and performed stochastic modeling on the basis of maximum likelihood and the information theoretic approach (Burnham & Anderson 2002). Capture-mark-recapture methods supply relatively robust estimates of population demographic parameters and provide promising techniques for assessing the effects of endemic disease on populations. In these analyses, we assumed that the chance of encountering an individual on a particular occasion was a product of 2 or more apparent probabilities (survival φ, recapture ρ, population growth λ, and recruitment *f*), which may be affected by predictor variables (e.g., infection status or environmental, linear, or individual covariates).

Analysis included defining biological questions, a priori hypotheses and estimable parameters; determining biologically plausible predictor variables; testing goodness of fit from general mark-recapture assumptions for the most parameterized models to determine an overdispersion parameter $\hat{c}$; specifying candidate model sets; selecting parsimonious models using small sample size and overdispersion-corrected quasi-Akaike's information criterion ($QAIC_c$); and performing multimodel inference via model averaging. We specify parameter and unconditional precision estimates (95% CIs), relative factor importance, evidence ratios of support between models for inference about certain hypotheses, and the model averaged effect sizes of infection status groupings where applicable.

We sought to determine the growth rates of the populations, and the importance of Bd and other covariates (environmental or individual) on survival and recruitment probabilities. These questions are associated with hypotheses that relate to estimable parameter probabilities (adult local apparent survival probability [φ] confounded by permanent emigration, recapture probability[ρ], population growth [λ], and recruitment probability [*f*] confounded by permanent immigration) and biologically plausible predictor variables, including infection status at first capture (binary grouping variable, *g*), seasonally varying environmental covariates (temperature, rainfall, relative humidity, and radiation), linear variables (apparent trip prevalence; cyclical seasonal linear trend; noncyclic linear trend, and capture effort [d]), and a static individual covariate (snout-urostyle length as proxy for age) (Dochtermann & Jenkins 2011) (Supporting Information). We performed mark-recapture modeling with Program Mark (version 6, build 6002) (White & Burnham 1999). We used the Cormack-Jolly-Seber (CJS) open population live-recaptures only approach for basic analysis and reverse time Pradel models (Pradel 1996) to determine realized population growth rate (λ) and recruitment (*f*). We performed single imputation of population means for missing values. Females and juveniles were excluded from CMR analyses due to infrequent presence at the stream. A monthly temporal scale was used for data input; hence, parameters were estimated as monthly probabilities (where 1 month $= \frac{365}{12} \approx 30.42$ days). Candidate model sets for CJS and Pradel analyses for each study site were separately constructed a priori via a restricted form of the all subsets approach and tested systematically (Lukacs et al. 2010; Hegyi & Garamszegi 2011; Doherty et al. 2012) (Supporting Information). The number of variables was small relative to sample size to avoid Freedman's paradox (Lukacs et al. 2010). Fixed-effects models demonstrated superior parsimony to random effects models and hence were used exclusively in these analyses.

Several assumptions must be fulfilled for CMR analyses to be applied without bias (Lebreton et al. 2009; Lindberg 2012). Toe-tip marks were permanent in adults for the study duration, and every effort was made to identify them correctly. Sampling time was negligible relative to sampling intervals. Two further assumptions relate to individual heterogeneity (in capture and survival probabilities), and these were formally addressed with goodness-of-fit tests on the most general model in the candidate set, from which the overdispersion parameter $\hat{c}$ was calculated ($\hat{c}$ = 1.145, 1.098 for Tully and Kirrama CJS analyses respectively [Supporting Information]).

RESULTS

Population and disease summary statistics

The observable population of adult common mist frogs was larger at Tully (302 frogs) than at Kirrama (88 frogs; Table 1). However, in both populations only 23 females were observed (Table 2). At Tully, although statistical significance was precluded by few captures, infection trends in captured females suggested higher infection prevalence (59% compared with 37% of males infected at first capture) and higher infection intensity than in males (mean zoospore load of 415 zoospore equivalents compared with 40 zoospore equivalents in males). In addition, 3 of the 4 clinically infected frogs that died on capture during the study period were females. No amplexing pairs were observed; however, males were calling and possessed nuptial pads year round, and females were observed at the stream May-August.

Chytridiomycosis infection prevalence for each trip varied seasonally in both populations with highest prevalence during winter months (Table 3). There was a strong negative correlation between apparent prevalence and mean daily maximum temperature of the 28 days preceding each trip at Tully (Spearman's correlation coefficient -0.894, $p \leq 0.0005$, $n = 21$ sampling trips for CMR analyses) (Fig. 1). At Kirrama infection prevalence had low precision due to infrequent captures, but it varied seasonally (Table 3 & Supporting Information). Adult males appeared to maintain territories at both sites and rarely migrated within the study site; location for recaptured frogs (mean first recapture interval 72.3 days, median 45.5 days for Tully; mean interval 101.9 days, median 90 days for Kirrama) correlated strongly with location at initial capture (Spearman's correlation coefficient 0.877, $p \leq 0.0005$, $n = 128$ for Tully; 0.807, $p \leq 0.0005$, $n = 37$ for Kirrama).

Mark-Recapture modeling

Model-averaged parameter estimates revealed clear seasonality in apparent survival, population growth, and recruitment probabilities (Figs. 2, 3 & Supporting Information). Evidence ratio support for seasonal effects was strong at Tully (in a comparison of most parsimonious models of temporal constancy dot [.] or nonseasonal *d* models with seasonal effects models, ratios were 1134.3, 40614, and 35329 for survival, population growth, and recruitment respectively), which correlated with limited to moderate support at Kirrama (1.8306, 25.580, and 1.0379 for survival, population growth, and recruitment respectively) (Lukacs et al. 2007). There was no evidence for a seasonal effect on recapture probability at either site (most parsimonious models contained the variable capture effort *d* but not seasonal effects).

Apparent infection prevalence at each trip correlated negatively with and was the most important predictor variable for survival at Tully (relative predictor variable importance, reporting only those >0.1, was prevalence 0.6287, temperature 0.1688, and seasonal trend 0.1262) (Fig. 2a). Sparse data at Kirrama precluded the usefulness of prevalence as a variable with that population (low precision) (Table 3); however, apparent survival estimates followed a similar seasonal trend to those at Tully (relative importance of predictors for survival were seasonal trend 0.2215, temperature 0.1707, rainfall 0.1217 and prevalence 0.1176) (Fig. 3a). There was predictor selection uncertainty for recapture at Tully (*d* 0.2891, relative humidity 0.2154, and radiation 0.1283) (Fig. 2b); however, the number of capture nights per trip was an important predictor for recapture probability at Kirrama (*d* =0.9060) (Fig. 3b). Population growth at Tully was best described by a positive association with relative humidity at Tully (relative humidity 0.8376 and prevalence 0.1187) (Fig. 2c) and a seasonal linear trend in which spring was considered equivalent to autumn, at Kirrama (seasonal trend 0.6301 and temperature 0.2327) (Fig. 3c).

Despite seasonality, average annual survival probability over the study period (derived from daily model-averaged estimates interpolated via third-order piecewise polynomial) was 0.12 (95% CI 0.02-0.30) for Tully and 0.15 (95% CI 0.00-0.60) for Kirrama (from CJS candidate model sets). Annual recruitment was similarly 0.91 (95% CI 0.83-0.96) for Tully and 0.71 (95% CI 0.31-0.98) for Kirrama. Population growth fluctuated seasonally during the study period (Figs. 2c & 3c). The values above and the equation $\lambda = \varphi + f$ indicate that annual population growth was 1.03 (95% CI 0.84-1.26) for Tully and 0.85 (95% CI 0.31-1.58) for Kirrama, which suggests equivocal results for gradual decline in the latter. There was little apparent effect of Bd infection status at first capture on survival or recapture at both Tully and Kirrama (model-averaged effect size 95% CI for difference between group parameter estimate means contained zero).

DISCUSSION

Our results suggest that more than 15 years after the arrival of Bd in the region, chytridiomycosis continued to be an important cause of frog mortality at the population level. At our lowland study sites, however, high recruitment appeared to compensate for this high apparent annual adult mortality and resulted in population growth rates that fluctuated seasonally during the study period. The necessity for increased recruitment (or immigration) to maintain populations at their current size potentially renders these populations vulnerable to stochastic events and other threatening processes. Thus, these populations may still be threatened by endemic chytridiomycosis.

Chytridiomycosis prevalence and apparent survival

Apparent annual male survival probabilities were low at both study sites. Our results were limited to the male subpopulation for logistical reasons; thus, gender differences may contribute to biased interpretation, particularly if female survival has more effect on population persistence than male survival. Our occasional observations of females, however, suggested non significant trends in survival similar to, if not greater in effect than those of the male subpopulation. Our results suggested chytridiomycosis was the cause of high apparent winter mortality in both years despite infrequent detection of dying frogs. Linking population-level measures throughout and between years, Bd infection prevalence was the best predictor of apparent survival probability. Apparent Bd prevalence at Tully was almost 4 times as well supported as temperature and the other putative predictors including environmental covariates and snout-urostyle length. Although the results for Kirrama were not similarly clearly linked to prevalence, we suggest that limited recaptures reduced precision of the prevalence measure in this population and led to lower model parsimony, although the general trends in apparent survival were similar.

Our findings are consistent with those of previous studies conducted in other bioregions, which indicates the negative effect of endemic chytridiomycosis on frog populations. These studies demonstrate reduced individual survival probability due to infection (Murray et al. 2009), and that infected populations can have lower growth rates than comparable naive populations (Pilliod et al. 2010).

Seasonality and Breeding Season

Seasonality of both infection prevalence and various demographic parameters (such as survival) at our sites is consistent with results of previous studies on chytridiomycosis (Kriger & Hero 2006) and was likely driven by climate (Altizer et al. 2006). Seasonal weather changes drive patterns in resource availability, host factors (behavior, immune function and contact rates) (Rachowicz & Vredenburg 2004; Rowley & Alford 2007; Ribas et al. 2009), and pathogen factors (abundance, distribution and growth rates) (Piotrowski et al. 2004). Our finding of a strong negative correlation between prevalence and temperature is consistent with previous evidence that suggests an optimal range of temperatures for Bd growth (17-25°C) (Forrest & Schlaepfer 2011). The correlations between temperature, prevalence, and survival we found are consistent with the loss of high-elevation populations of common mist frogs that coincided with the regional emergence of Bd (McDonald & Alford 1999). Temperature is likely an important mechanistic driver of infection prevalence in our susceptible range-contracted but currently nondeclining endemic system, and in turn, prevalence was an important driver of seasonal adult mortality.

The presence of transient females and high male abundance at the stream during May-August (autumn and winter) suggests this was the breeding season, and the correlated capture locations of resident males between sampling trips was consistent with the maintenance of territories (Hodgkison & Hero 2002). In a separate but related study, common mist frog tadpoles were observed at the stream year-round, but predominantly May-January (S. D. C. unpublished data). We also identified high-capture deviance residuals during early winter (Supporting Information), which suggests the presence of transient individuals during the breeding season (although these sampling trips were necessarily excluded from CMR analyses). The higher winter prevalence could thus also be caused by the increased potential for infection transmission due to higher host densities during the breeding season.

Management implications

Understanding the effect of endemic Bd on demographic parameters has important implications for short-term management strategies and the longer-term potential for evolution of host resistance, particularly where apparent annual host survival is low. We speculate that if reproduction during the breeding season occurs prior to or during the subclinical phase of infection and is followed by high adult mortality, then selection for resistance to Bd may have less opportunity to manifest between generations. Despite evidence for species, population, and individual differences in susceptibility to chytridiomycosis (Tobler & Schmidt 2010; Searle et al. 2011), to date only one study has demonstrated evidence for intergenerational selection for resistance to infection (Savage & Zamudio 2011). Population dynamics such as those described above may contribute to slowing the evolution of resistance to chytridiomycosis, particularly where infection is not vertically transmitted and juveniles favor terrestrial foraging sites, which reduces their prebreeding infection risk (Hodgkison & Hero 2002).

High apparent mortality of the reproductive subpopulation additionally forces dependence on seasonal recruitment of juvenile or immigrating males (consistent with high recruitment found here). Without baseline demographic data (due to the absence of Bd-naive populations), we speculate that these infected populations may be facing physiological boundary thresholds for their reproductive capacity, as demonstrated by Pilliod et al. (2010) and Muths et al. (2011), and may be at lower abundance than if the disease were absent. Depending on meta-population connectivity, resource quality, and the presence of other synergistically acting threatening processes, these populations may have increased vulnerability to stochastic perturbations (such as drought and cyclones). We suggest use of adaptive management strategies to improve understanding of the degree of threat imposed by endemic chytridiomycosis (Woodhams et al. 2011). Comparing demographic responses between sites where active management has been undertaken and untreated sites may elucidate the capacity of these populations to recover from infection pressure or accommodate additional stressors. Reducing seasonal mortality may relieve the necessity for high recruitment or increase baseline population abundance.

Study uncertainties

We were unable to quantify mortality attributable to chytridiomycosis in this study because there was no apparent effect of infection status at first capture on survival or recapture probability. This was not unexpected because in the field the infection is frequently gained and lost through time (consistent with Briggs et al. 2010). The use of time-varying individual covariates and multistate designs (Murray et al. 2009) is currently precluded for Pradel analyses, although methods may soon be developed (Lebreton et al. 2009). In addition, the use of highly sensitive diagnostic tests and the short time course and high mortality of clinical disease meant that ill individuals comprised only a small proportion of the captured subpopulation (moribund frogs were rarely observed) (Cooch et al. 2012). Inference was thus limited to the observable population which in this case largely excluded the moribund class and females and juveniles. Additional limitations of the study include our use of spatially interpolated climatic variables, which meant we could not account for small-scale habitat factors (Jeffrey et al. 2001; BOM 2008), and possible effects of toe-tipping on both survival and recapture probabilities (Phillott et al. 2010a).

Apparent survival probabilities are confounded with permanent emigration in mark-recapture studies (Murray et al. 2010b). However, our study extended across years, and we found high site fidelity in recaptured males (45% of the male population). This finding reduced the likelihood of emigration confounding. Moreover, periods of lowest apparent survival corresponded with the influx (or higher visibility) of transient males during the breeding season, so confounding of survival by emigration is a less plausible explanation. In addition, we speculated that predominantly subclinical infection prevalence is unlikely to be a good predictor of emigration probability due to the absence of marked physiological changes, although further research into effects of subclinical chytridiomycosis on frog behavior is warranted.

Our results suggest that even in the absence of observed mortalities and continued declines, endemic chytridiomycosis may have important seasonally fluctuating population-level effects on amphibian survival. The low apparent survival probability of adult common mist frogs necessitates increased annual recruitment for population persistence. Seasonal mortality of reproductive adults may also have implications for the long-term evolution of resistance to chytridiomycosis. We found that seasonal increases in prevalence negatively affected survival, despite host-pathogen coexistence for multiple host generations, and this finding suggests that these and similar endemically infected populations may be under continued threat from chytridiomycosis and thus may be vulnerable to other threatening processes, particularly those affecting recruitment success.

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SUPPORTING INFORMATION

Detailed information about predictor variables, goodness-of-fit testing, construction of candidate model sets and abbreviated tables of results are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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TABLES

Table 1. Encounter distribution summary of adult common mist frogs grouped by study site.

Study site	Capts[a]	Frogs[b]	Frogs captured > 1[c]	Range of capts per trip[d]	Max encounters[e]	Max period (days)[f]
Tully	535	302	128	7-53 (May 2007)	10	309
Kirrama	151	88	37	3-22 (May 2006)	5	506

[a]Total number of captures. [b]Total number of frogs captured. [c]Number of frogs captured more than once. [d]Month and year when highest number of frogs were observed in parentheses. [e]Maximum number of encounters recorded for any frog. [f]Maximum period over which an individual frog was observed.

Table 2. Number of male, female, and gender indeterminate adult common mist frogs captured.

Study site	Male (% total)[a]	Female (% total)	Unknown (% total)[b]	Total
Tully	284 (94.0)	16 (5.3)[c]	2 (0.7)	302
Kirrama	73 (83.0)	7 (8.0)[d]	8 (9.1)	88
Total	357	23	10	390

[a] Numbers in parentheses are percentages of total frogs per site. [b] Gender undetermined. [c] One female was recaptured. [d] No females recaptured.

Table 3. *Batrachochytrium dendrobatidis* (Bd) infection prevalence (prev) in adult common mist frogs.

Study site	Prev range (%)[a]	Lowest prev[b]	Highest prev[c]	Positive PCR tests (total tests)	Mean zoospore load (range)	SD[d]	Median[e]
Tully	5.3-65.4	February 2006	August 2007	193 (530)	28 (0-4028)	210.2	0
Kirrama	0.0-59.3	many[f]	July 2006	46 (148)	65.88 (0-4232)	479.0	0

[a] Range in point Bd infection prevalence measured per trip as percentages (Supporting Information). [b] Month and year when the lowest prevalence was recorded. [c] Month and year when the highest prevalence was recorded. [d] Standard deviation of common mist frog zoospore loads. [e] Median common mist frog zoospore load. [f] Across-species trip prevalence at Kirrama was recorded as 0.0 during 4 of 18 sampling trips.

FIGURE LEGENDS

Figure 1. Apparent chytridiomycosis infection prevalence of adult male common mist frogs (Supporting Information), daily maximum temperatures (Temp Max) over the study period (from the end of the first survey interval), and mean daily maximum temperature for the 28 days preceding each trip (Temp Mean) at an unnamed creek in Tully Gorge National Park. Prevalence error bars are the 95% confidence interval of a proportion from the binomial distribution (dependent on sample size).

Figure 2. Model-averaged estimates for monthly (a) survival probability, (b) recapture probability, and (c) population growth rate and recruitment probabilities with unconditional 95% confidence intervals from the Cormack-Jolly-Seber and Pradel analyses respectively for adult male common mist frogs at an unnamed creek in Tully Gorge National Park. The respective most highly supported predictor variables accompany each parameter probability curve for comparison (prevalence, apparent chytridiomycosis prevalence; capture effort, capture effort per trip; relative humidity, mean relative humidity 28 days preceding each sampling trip [Supporting Information]). Points on the graph for trip sessions have been staggered horizontally where necessary for clarity, initial values correspond temporally with the end of the first survey interval, and a straight-line interpolation has been added between estimates for visual comparison of trends.

Figure 3. Model averaged estimates for monthly (a) survival probability, (b) recapture probability, and (c) population growth rate and recruitment probabilities with unconditional 95% confidence intervals from the Cormack-Jolly-Seber and Pradel analyses respectively for adult male common mist frogs at Bridge 7 in Kirrama National Park. The respective most highly supported predictor variables accompany each parameter probability curve for comparison

(temperature, mean daily maximum temperatures of 28 days preceding each trip; seasonal trend, cyclical seasonal trend [spring considered equivalent to autumn]; capture effort, capture effort per trip [Supporting Information]). Points on the graph for trip sessions have been horizontally staggered where necessary for clarity, initial values correspond temporally with the end of the first survey interval, and a straight-line interpolation has been added between estimates for visual comparison of trends.

Figure 1.

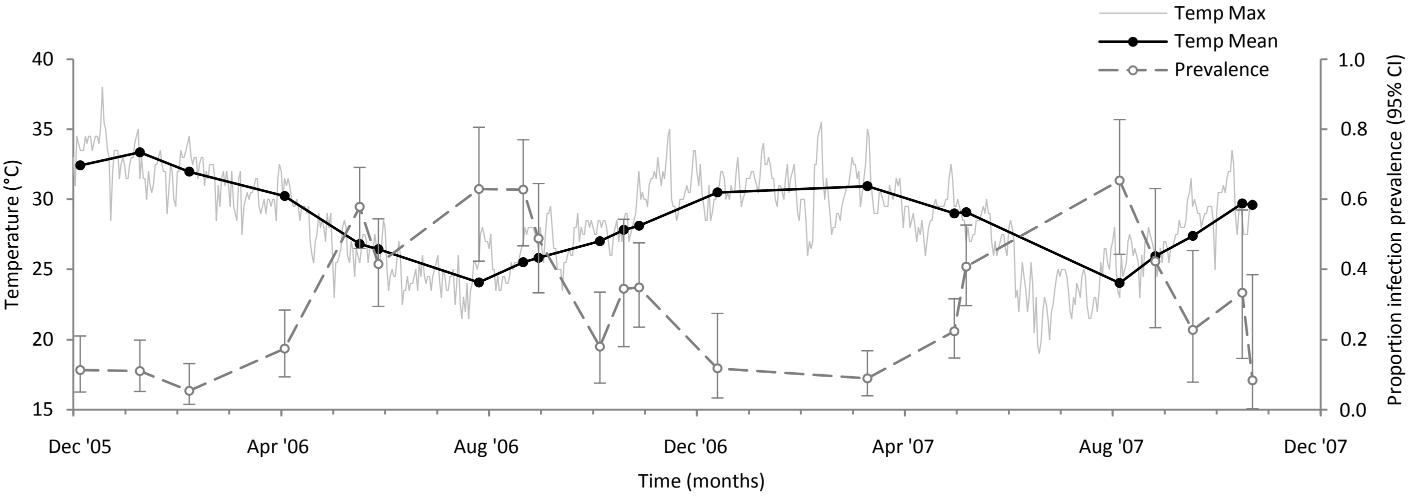

Temp Max
Temp Mean
Prevalence
Temperature (°C)
Proportion infection prevalence (95% CI)
40
35
30
25
20
15
1.0
0.8
0.6
0.4
0.2
0.0
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
Time (months)

Figure 2.

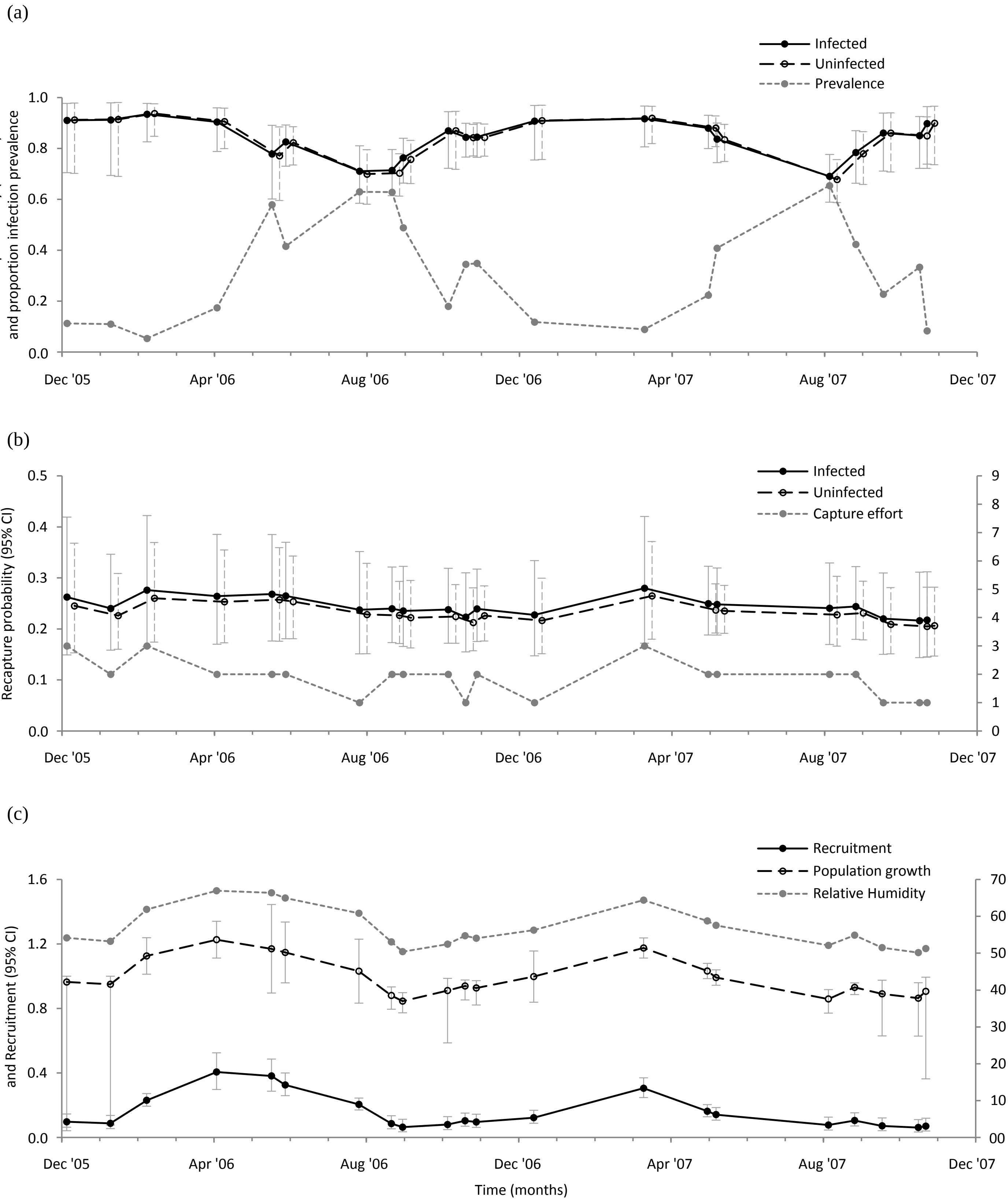
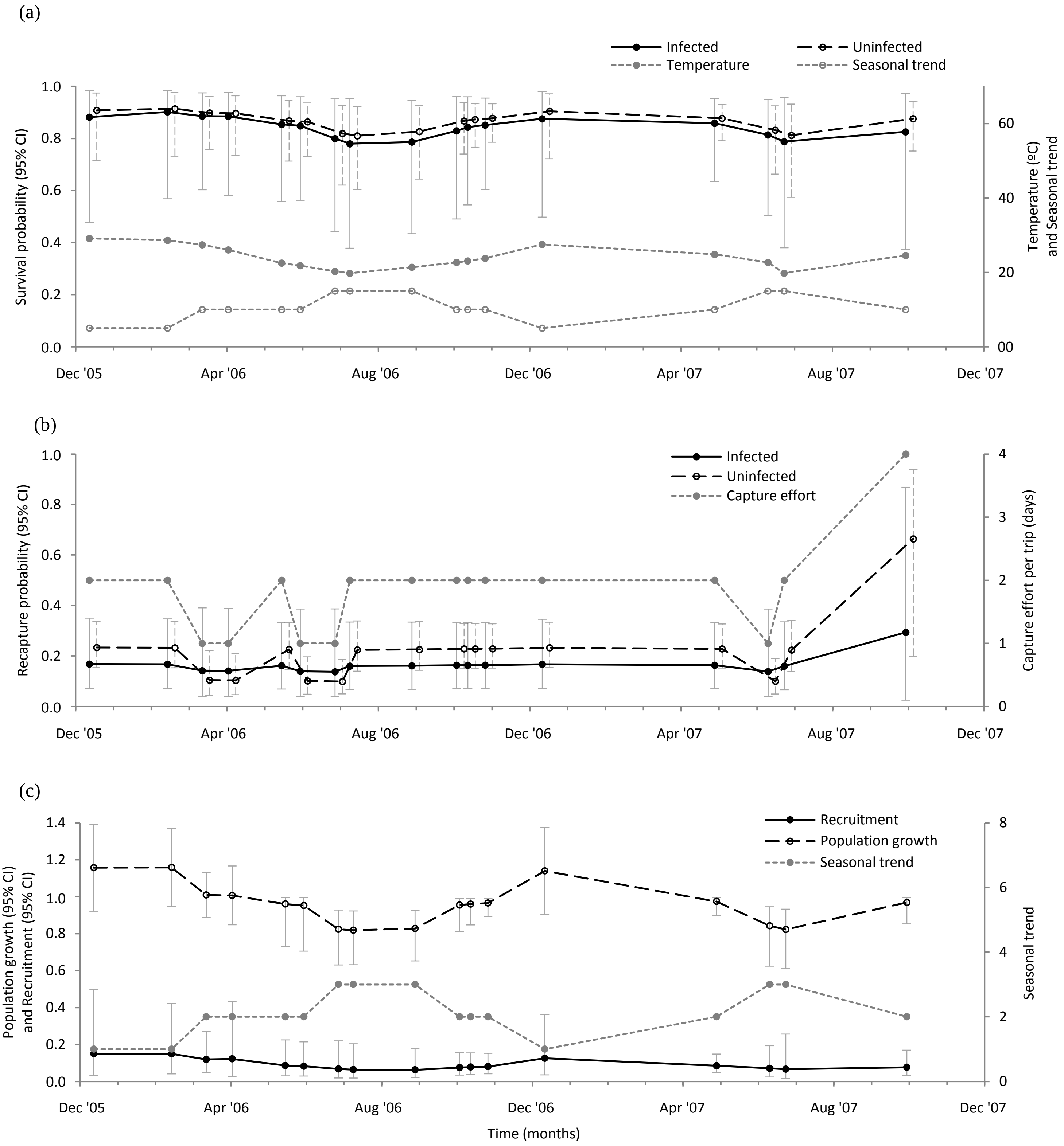

(a)
Infected
Uninfected
Prevalence
Survival probability (95% CI) and proportion infection prevalence
1.0
0.8
0.6
0.4
0.2
0.0
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
(b)
Infected
Uninfected
Capture effort
Recapture probability (95% CI)
0.5
0.4
0.3
0.2
0.1
0.0
Capture effort per trip (days)
9
8
7
6
5
4
3
2
1
0
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
(c)
Recruitment
Population growth
Relative Humidity
Population growth (95% CI) and Recruitment (95% CI)
1.6
1.2
0.8
0.4
0.0
Relative humidity (%)
70
60
50
40
30
20
10
00
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
Time (months)

Figure 3.


(a)
Infected
Uninfected
Temperature
Seasonal trend
Survival probability (95% CI)
1.0
0.8
0.6
0.4
0.2
0.0
Temperature (ºC) and Seasonal trend
60
40
20
00
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
(b)
Infected
Uninfected
Capture effort
Recapture probability (95% CI)
1.0
0.8
0.6
0.4
0.2
0.0
Capture effort per trip (days)
4
3
2
1
0
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
(c)
Recruitment
Population growth
Seasonal trend
Population growth (95% CI) and Recruitment (95% CI)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Seasonal trend
8
6
4
2
0
Dec '05
Apr '06
Aug '06
Dec '06
Apr '07
Aug '07
Dec '07
Time (months)