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RESEARCH ARTICLE

Interpopulation differences in male reproductive effort drive the population dynamics of a host exposed to an emerging fungal pathogen

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Abstract

1. Compensatory recruitment is a key demographic mechanism that has allowed the coexistence of populations of susceptible amphibians with *Batrachochytrium dendrobatidis* (Bd), a fungus causing one of the most devastating emerging infectious disease ever recorded among vertebrates. However, the underlying processes (e.g. density-dependent increase in survival at early life stages, change in reproductive traits) as well as the level of interpopulation variation in this response are poorly known.
2. We explore potential mechanisms of compensatory recruitment in response to Bd infection by taking advantage of an amphibian system where male reproductive traits are easy to quantify in free-living populations. The Southern Darwin's frog *Rhinoderma darwinii* is a vocal sac-brooding species that exhibits a high susceptibility to lethal Bd infection.
3. Using a 7-year capture-recapture study at four populations with contrasting Bd infection status (one high prevalence, one low prevalence and two Bd-free populations), we evaluated whether Bd-positive populations exhibited a higher adult recruitment and a higher male reproductive effort than Bd-negative populations. We also estimated population growth rates to explore whether recruitment compensated for the negative impacts of Bd on the survival of adults. In addition, we evaluated a potential demographic signal of compensatory recruitment (i.e. positive relationship between the proportion of juveniles and Bd prevalence) in response to Bd infection using raw count data from 13 *R. darwinii* populations.

4. The high Bd prevalence population exhibited the highest male reproductive effort and the highest recruitment among the four monitored populations. This led to a growing population during the study period despite high mortality of adult hosts. In contrast, males from the population with low Bd prevalence had a low reproductive effort and this population, which had the lowest adult recruitment, was declining during the study period despite adults having a higher survival in comparison to the high Bd prevalence population. We also found a demographic signal of compensatory recruitment in response to Bd infection in our broader analysis of 13 *R. darwinii* populations.
5. Our study underlines the importance of interpopulation variation in life-history strategies on the fate of host populations after infectious disease emergence. Our results also suggest that an increase in reproductive effort can be one of the processes underlying compensatory recruitment in populations of Bd-susceptible amphibians.

KEYWORDS

Chile, chytridiomycosis, fecundity compensation, host–parasite system, life history, pace of life

1 | INTRODUCTION

Empirical examples from a wide range of host species illustrate the devastating effects of emerging infectious diseases on wildlife (e.g. Daszak et al., 2000; Frick et al., 2015). Yet, population collapse is not the only outcome from emerging host–parasite interactions. Some populations of susceptible hosts can persist despite an initial but transient population decline (e.g. fish, Rogowski et al., 2020; amphibians, Briggs et al., 2010; marsupials, Wells et al., 2019). A better understanding of the demographic processes determining population-level responses following infectious disease emergence is a critical step to predicting threat outcomes and to designing effective mitigation strategies (West et al., 2020).

Recent examples in wild vertebrates support theoretical expectations that susceptible hosts can reduce population-level impacts of infectious disease through demographic compensation (Jones et al., 2008; Lampo et al., 2017; Lazenby et al., 2018; McDonald et al., 2016; Muths et al., 2011; Rogowski et al., 2020; Valenzuela-Sánchez et al., 2021). For instance, an increase in recruitment into the adult stage can compensate for the disease-induced increase in adult mortality, preventing population decline (i.e. compensatory recruitment; McDonald et al., 2016; Rogowski et al., 2020; Valenzuela-Sánchez et al., 2021). Compensatory recruitment can occur via three different mechanisms: (a) a non-specific response arising from the effect of infectious disease on host population density (i.e. density-dependent compensatory recruitment; McDonald et al., 2016; Rogowski et al., 2020); (b) plasticity in reproductive traits triggered by an increased mortality risk (Agnew et al., 2000; Stearns, 1989); and (c) rapid evolution of reproductive traits (Hochberg et al., 1992; Koella & Restif, 2001). Indeed, parasites are ubiquitous in nature, exert selective pressures on their hosts and drive the expression of

host life histories (Hochberg et al., 1992; Koella & Restif, 2001). For instance, either by increasing mortality risk or by reducing future reproduction, parasites can alter the trade-off optimum between current and future reproduction such that, to optimize lifetime reproductive success, hosts might need to increase current reproductive effort (Duffield et al., 2017).

The amphibian *Batrachochytrium dendrobatidis* (Bd) system provides an excellent opportunity to improve our understanding of compensatory recruitment in response to emerging infectious diseases in wild populations. The chytrid fungus *Batrachochytrium dendrobatidis* causes amphibian chytridiomycosis, a lethal disease that has contributed to the decline of 501 amphibian species, including the potential extinction of 90 species (Scheele, Pasmans, et al., 2019). Extensive research on amphibian Bd systems, including several long-term studies aimed at elucidating the impacts of Bd on amphibian population dynamics (e.g. Briggs et al., 2010; Muths et al., 2011; Russell et al., 2019), has shown that the population-level effects of Bd infection are highly variable at both the interspecific and intraspecific levels (e.g. Briggs et al., 2010; Hossack et al., 2020). Importantly, there is increasing evidence that compensatory recruitment is a key mechanism allowing population persistence of Bd-susceptible hosts (Brannelly et al., 2021; Lampo et al., 2017; Muths et al., 2011; Scheele et al., 2015; West et al., 2020). However, the underlying processes (e.g. density-dependent increase in survival at early life stages, change in reproductive traits) as well as the level of interpopulation variation in this response are poorly known (Brannelly et al., 2021). This knowledge gap can be partially attributed to the fact that some parameters, such as reproductive effort or survival rates of early life stages, are not easy to quantify in free-living amphibian populations (Petrovan & Schmidt, 2019).

To overcome this limitation, we take advantage of an amphibian system where reproductive traits are easy to measure in free-living populations. The Southern Darwin's frog *Rhinoderma darwinii* is a fully terrestrial amphibian in which the larval stage occurs within the male's vocal sac (Valenzuela-Sánchez et al., 2014). The presence and number of developing larvae is externally visible in this species (Serrano et al., 2020). Thus, male reproductive effort, in terms of frequency of brooding attempts and number of brooded larvae, can be estimated using field data. Also, this species is highly susceptible to lethal Bd infection (Valenzuela-Sánchez et al., 2017) and Bd has been proposed as one of the main drivers of its widespread decline and of the possible extinction of its sister species, *R. rufum* (Azat et al., 2021; Soto-Azat, Valenzuela-Sánchez, Clarke, et al., 2013).

Using a 7-year capture–recapture study and a set of demographic analyses in four *R. darwinii* populations with contrasting Bd infection status, we ask whether males from Bd-positive populations exhibited a higher reproductive effort than males in Bd-negative populations. Subsequently, we evaluated whether Bd-positive populations exhibited a comparatively higher rate of adult recruitment that might compensate for an increased mortality rate. We also investigated other life-history metrics that could account for potential interpopulation differences in life-history strategies and population responses to Bd infection in *R. darwinii*. The position of a species or population on the slow–fast life-history continuum can modulate host responses to parasitism, including the mechanisms and strength of compensatory response (Valenzuela-Sánchez et al., 2021). For example, compensatory recruitment seems to be less common in slow than in fast life-history strategies (Valenzuela-Sánchez et al., 2021). We used generation time as a proxy of the position of our studied populations along the slow–fast life-history continuum (Valenzuela-Sánchez et al., 2021) and assumed that populations towards the slow end of the continuum have a longer generation time (Gaillard et al., 2005). Finally, we expanded our analysis to 13 *R. darwinii* populations to look for a demographic signal of compensatory recruitment in response to Bd infection across a broader array of populations.

2 | MATERIALS AND METHODS

2.1 | Capture–recapture study

2.1.1 | Study design

From 2014 to 2020, we carried out a capture–recapture (CR) study of four *R. darwinii* populations in Chile (Figure 1): Monumento Natural Contulmo ('CON'), Reserva Biológica Huilo Huilo ('HUI'), Parque Tantauco ('TAN') and Reserva Natural Melimoyu ('MER'). The study incorporated two nearby plots per population. These populations are within native old-growth forests of similar characteristics, where no other anthropogenic stressors besides Bd are known to occur (Azat et al., 2021). The CR data were collected at two nested levels of capture occasions (i.e. Pollock's robust design; Pollock, 1982). Each year, we carried out one primary survey period in early summer

during the peak of the reproductive season (January–February). During each of these primary periods, we performed three or four secondary survey occasions, that is, each plot was surveyed daily on three or four consecutive days (Table 1).

Details on searching and handling methodology have been extensively described in previous studies (Valenzuela-Sánchez et al., 2014, 2017). Briefly, all captured frogs were measured (Snout-to-vent length, SVL), photographed for individual recognition using their ventral colouration patterns and released at the exact point of capture (Valenzuela-Sánchez et al., 2017). Adults were sexed based on morphological characteristics (i.e. presence of vocal sac in calling and brooding males and enlargement of the coelomic cavity in gravid females; Valenzuela-Sánchez et al., 2014).

2.1.2 | Population Bd infection status

The Bd infection status of these four populations was determined based on 1,690 skin swabs collected from 2014 to 2019 (CON, $n = 285$, HUI = 690, TAN = 633, MER = 82; further details on the methods used for the detection of Bd DNA are provided in Soto-Azat, Valenzuela-Sánchez, Clarke, et al. (2013)). *Batrachochytrium dendrobatidis* infection was not found in TAN or MER; therefore, we classified these as Bd-free populations. In CON, 11.1% (19/171) of the frogs were identified as Bd infected in at least one year, while in HUI it was 6.4% (19/314). Therefore, CON was classified as having a high Bd infection prevalence and HUI a low Bd infection prevalence (see discussion in Valenzuela-Sánchez et al. (2017) about why true prevalence may be largely underestimated in our system). In agreement with our Bd status classification, an intensive CR study conducted during 2018–2019 at the two Bd-positive populations revealed that the probability of acquiring a Bd infection was 3.5 times higher in frogs from CON than in HUI (Haddow-Brown, 2019).

2.1.3 | Male reproductive effort

We analysed two male reproductive parameters: the annual probability of brooding larvae and the number of offspring produced. To calculate the former, we used a multistate CR model (Lebreton et al., 2009) with two states according to the observed reproductive status of captured adult males [brooding males (BM) or non-brooding males (M)]. We denoted the transition probability from the M to the BM state as ψ_{M-BM} , and the transition probability from the BM to the M state as ψ_{BM-M} . Then, we calculated brooding probability as $\psi_{M-BM}/(\psi_{M-BM} + \psi_{BM-M})$, that is, the annual probability for a male in the population to be in the brooding state. Due to sparse male CR data at each population, we constructed only a simple model where both transition probabilities were modelled as time constant, but population specific. We allowed population-specific recapture probabilities to vary among years. For this analysis only, we pooled CR observations from secondary capture occasions into a single capture occasion per year; the multistate model used

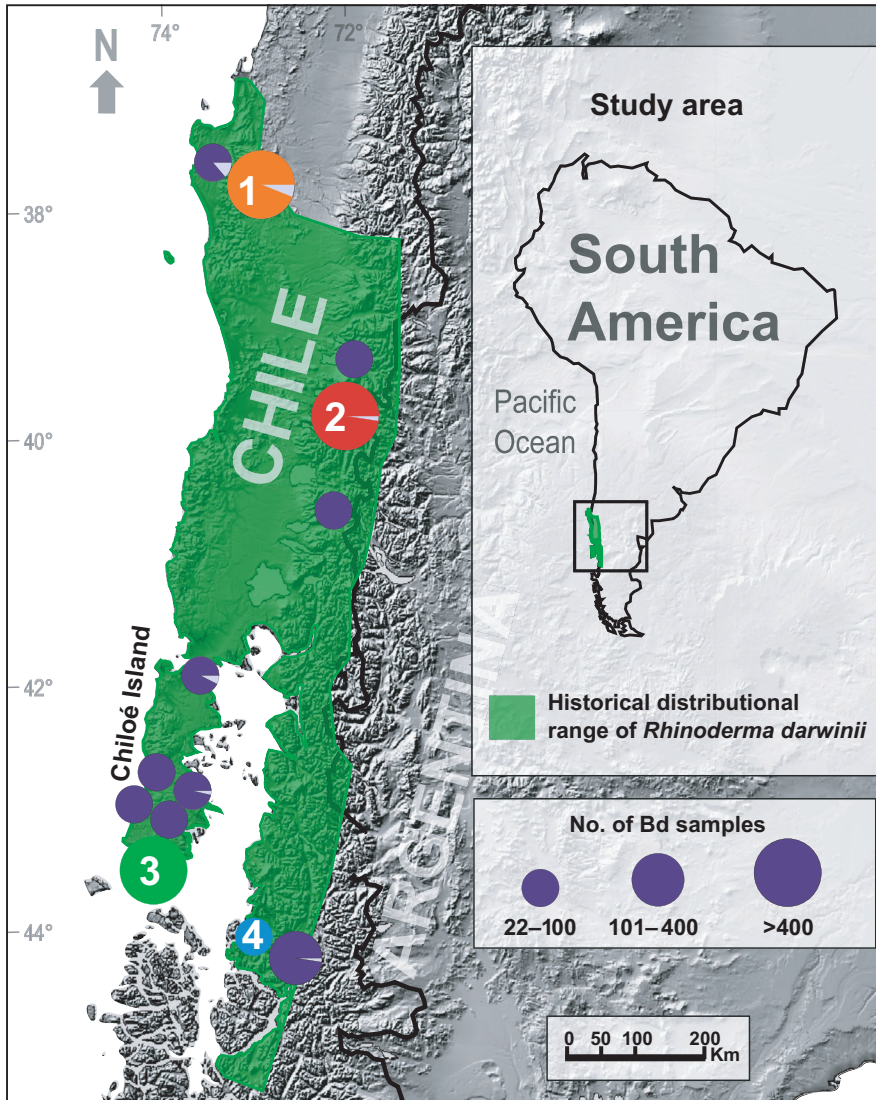


FIGURE 1 Study area and *Batrachochytrium dendrobatidis* (Bd) infection prevalence at the 13 Southern Darwin's frogs *Rhinoderma darwinii* populations surveyed in this study in Chile. The numbered circles represent the four populations included in the capture–recapture study: 1 = Contulmo ('CON'), 2 = Reserva Biológica Huilo Huilo ('HUI'), 3 = Tantauco ('TAN') and 4 = Melimoyu ('MER'). The pale area within the circles represents the proportion of Bd-positive samples in each population

TABLE 1 Details of the 7-year capture–recapture study (2014–2020) performed at four populations of the Southern Darwin's frog *Rhinoderma darwinii* in Southern Chile

Site	CON	HUI	TAN	MER
No. survey periods ^a	7	7	7	7
Area surveyed (ha)	0.39	1.01	0.15	0.07
Search effort (h) ^b	16	32	16	16
No. captures	393	714	981	143
No. frogs	186	304	515	56
No. juveniles	109	79	209	33
No. adults	77	225	306	23
No. brooding males ^c	29	49	96	6

^aPrimary survey periods. Each survey period was composed of four consecutive days (secondary capture occasions) of survey with equal duration per day. Only in MER, the last primary survey period was composed of three secondary capture occasions.

^bSearch effort in person hours per primary survey period: two researchers conducted the survey on each occasion; search effort per survey period is expressed as the total in hours.

^cMales that were observed brooding larvae at least once during the study.

here does not deal with CR data collected under the robust design described above. The model was fitted to data in a Bayesian framework with uninformative priors, using JAGS through the R package JAGSUI (Kellner, 2015; Plummer, 2003; R Core Team, 2020). We ran three MCMC chains with 100,000 iterations, a burn-in of 10,000 and a thinning factor of 1. Chain convergence was evaluated using visual inspection of the chains and the Gelman–Rubin \hat{R} statistic (i.e. \hat{R} values < 1.1; Kéry & Schaub, 2012). We calculated differences in mean brooding probability between populations as derived quantities in the same multistate Bayesian model (i.e. effect estimates; Kéry, 2010).

To evaluate among-population differences in the number of offspring produced per male, we used a Bayesian Generalized Linear Model (GLM) with a Poisson error structure (Kéry, 2010) to model the number of larvae counted inside the male vocal sac as a function of population. The model was implemented in JAGS following Kéry (2010) using the same MCMC settings described above. As before, we calculated differences in mean number of larvae between populations as derived quantities in the same model (Kéry, 2010).

2.1.4 | Survival, recruitment and population growth rate

Subsequently, we used the Bayesian Jolly–Seber Robust Design (JSRD) model (Gibson et al., 2018) to estimate a set of demographic parameters within each of the four populations. At each population, we estimated the average apparent adult survival probability (hereafter, ‘survival probability’) to corroborate previous findings of a reduced survival probability in Bd-positive *R. darwinii* populations (Valenzuela-Sánchez et al., 2017). We also estimated mean recruitment to examine whether higher male reproductive effort resulted in higher recruitment. We specifically calculated per-capita recruitment, defined as the fraction of new adults at year t per adult alive at year $t - 1$. Finally, we calculated the annual population growth rate (λ_t) as N_{t+1}/N_t , where N_t is adult abundance at year t . To allow an easy comparison of the growth rates among populations, we estimated the geometric mean of the population growth rates across the 7-year period.

Briefly, the JSRD model is based on the open-population robust design model (Kendall & Bjorkland, 2001) and the multi-state Jolly–Seber superpopulation model (Kéry & Schaub, 2012). However, in contrast to the open-population robust design model of Kendall and Bjorkland (2001), the JSRD assumes population closure within primary occasions (Gibson et al., 2018). Within primary capture periods, we modelled detection probability as being constant across individuals and over time (corresponding to the model M_0 in classical closed CR models; Otis et al., 1978). Since we previously found time variation in recapture probability across primary capture periods in our study populations (Valenzuela-Sánchez et al., 2017), and to take into consideration different researchers performing fieldwork each year, we allowed this parameter to vary among primary capture periods. As survival usually displays negligible time-specific variation in *R. darwinii* (Valenzuela-Sánchez et al., 2017), and to facilitate spatial comparison of this parameter among populations with different exposure to Bd, survival probability was modelled as time constant.

Each population was analysed separately because the number of secondary survey occasions among populations at the last primary capture period was unequal. We fitted the JSRD model to CR data using the parameterization that follows an individual-level observation process (i.e. using the code provided in Data S3 in Gibson et al., 2018) through JAGS using the same MCMC settings described above. The code to reproduce this analysis is provided in Supporting Information.

2.1.5 | Matrix projection model

We constructed a pre-breeding census, age structured matrix population model (Caswell, 2001). The purpose of this model was twofold. First, we used this model to estimate generation time; this metric was used as a proxy of the position of the study populations along the slow–fast life-history continuum of life-history variation (i.e. longer generation time towards the slow end of the continuum; Gaillard et al., 2005). Second, we used an elasticity analysis

to evaluate the effect of proportional changes in any vital rate on the asymptotic growth rate for each population (Caswell, 2000). We constructed a simple life cycle for *R. darwinii* that considers three age classes: newborns, 1-year-old juveniles and adults. The survival component of newborns was incorporated into the fertility component of the projection matrix (see Kendall et al., 2019; Figure S3). Both newborns and 1-year-old juveniles remained in their respective age class for 1 year (corresponding to one time step in the model); all individuals are assumed to reach adulthood at the age of 2 years (Valenzuela-Sánchez et al., 2017). Accordingly, the 2×2 projection matrix was parameterized using the following vital rates shown in Table S1: (a) newborn annual survival probability; (b) juvenile annual survival probability, (c) adult annual survival probability and (d) annual per-capita fecundity (calculated as the product of the median number of larvae brooded by males and the proportion of brooding males in each adult population). We calculated lower-level elasticities from the projection matrix; the vital rate with the highest potential impact on the asymptotic population growth rate is the one with the highest elasticity (Caswell, 2000). Generation time was calculated as the inverse of the elasticity of the population growth rate to changes on fecundity (Bienvenu & Legendre, 2015). All the analyses were performed using the R package POPBIO v. 2.7 (Stubben & Milligan, 2007). Full model details, including code to replicate our results, are presented in the Supporting Information.

2.2 | Demographic signal of compensatory recruitment

We tested for an association between the proportion of juveniles (from raw count data) and Bd infection prevalence in 13 populations that were surveyed during 2009–2019 across southern Chile (Table S3). We predicted that recruitment compensation would lead to a positive relationship between the proportion of juveniles and Bd prevalence in the populations. Although the age structure can be biased towards the juvenile stage in Bd-positive populations if adults are more likely to die because of Bd infection than juveniles, in our model system both infection probability and Bd-induced mortality are similar in juveniles and adults (Haddow-Brown, 2019; Valenzuela-Sánchez et al., 2017).

The 13 study populations were distributed across the entire range of this species (Figure 1). All captures were made during the *R. darwinii* reproductive season (i.e. October–March; Azat et al., 2021). We defined the age class (juvenile or adult) of each captured frog based on its SVL (Valenzuela-Sánchez et al., 2017). Additionally, the skin surface of each captured individual was sampled using a sterile, dry swab for detection of Bd DNA ($n = 3,476$ skin swabs; further details in Soto-Azat, Valenzuela-Sánchez, Clarke, et al. (2013)). For this analysis, we defined the minimum sample size per population to be 22 individual frogs, which allows us to detect at least one Bd infection (if the pathogen was present in the population) assuming an expected prevalence of 12.5% (Soto-Azat, Valenzuela-Sánchez, Clarke, et al., 2013), a high test sensitivity of 99% (Boyle et al., 2004) and a 95% confidence level. We constructed a Bayesian binomial

GLM where the probability that a captured individual belongs to the juvenile stage (specifically, the probability of being a juvenile corresponded to the success probability, and the total number of individuals captured per population corresponded to the trial size of the binomial distribution; Kéry, 2010) was modelled as a function of Bd prevalence (Table S3). The model was implemented in JAGS following Kéry (2010) using the same MCMC settings described above.

3 | RESULTS

3.1 | Capture-recapture study

We attained a total of 2,231 captures of 1,061 different frogs (Table 1): 23.1% of the frogs were captured at least twice across different years (CON = 32 frogs, HUI = 83, TAN = 111, MER = 19). The adult dataset comprised 631 different frogs (Table 1), of which 29% were captured at least twice across different years (CON = 19 frogs, HUI = 71, TAN = 83, MER = 10). The sex ratio in adults was slightly male biased in the Bd-positive populations (ratio females to males, CON = 0.92; HUI = 0.97), and strongly male biased in the Bd-free populations (TAN = 0.56; MER = 0.55).

3.1.1 | Male reproductive effort

Males from the population with a high Bd prevalence (CON) had the highest reproductive effort, both in terms of brooding probability and the number of brooded larvae (Figure 2). The effect estimates

(Figure 2a) showed that mean brooding probability was higher in CON than in the population with low Bd prevalence (HUI) and without Bd (MER; and the Bayesian credible interval (CRI) of the difference in mean brooding probability between CON and the Bd-free population, TAN, only slightly overlapped zero). The number of larvae counted inside the vocal sac of captured males also differed among populations (Figure 2b). As indicated by the effect estimates, males in the population with high Bd prevalence brooded, on average, almost twice as many larvae as those in HUI, TAN and MER (Figure 2b).

3.1.2 | Survival, recruitment and population growth rate

Adult survival probability was the lowest in the high Bd prevalence population [CON = 0.465 (CRI = 0.336–0.605)]. By contrast, adult survival was relatively similar in populations with low Bd prevalence and without Bd [HUI = 0.596 (0.522–0.679); TAN = 0.577 (0.506–0.653); MER = 0.690 (0.505–0.872); Figure 3a].

Mean per-capita recruitment was highest in the population with high Bd prevalence (CON = 0.782 [0.675–0.956]), was slightly lower in one Bd-free population [TAN = 0.735 (0.618–0.876)] and lowest in the other Bd-free population [MER = 0.479 (0.317–0.781)] and the population with a low Bd prevalence [HUI = 0.398 (0.352–0.449); Figure 3b].

The population with high Bd prevalence (CON) was growing during the study period [mean population growth rate = 1.077 (1.044–1.115); Figure 3c]. Both Bd-free populations may have been slowly declining,

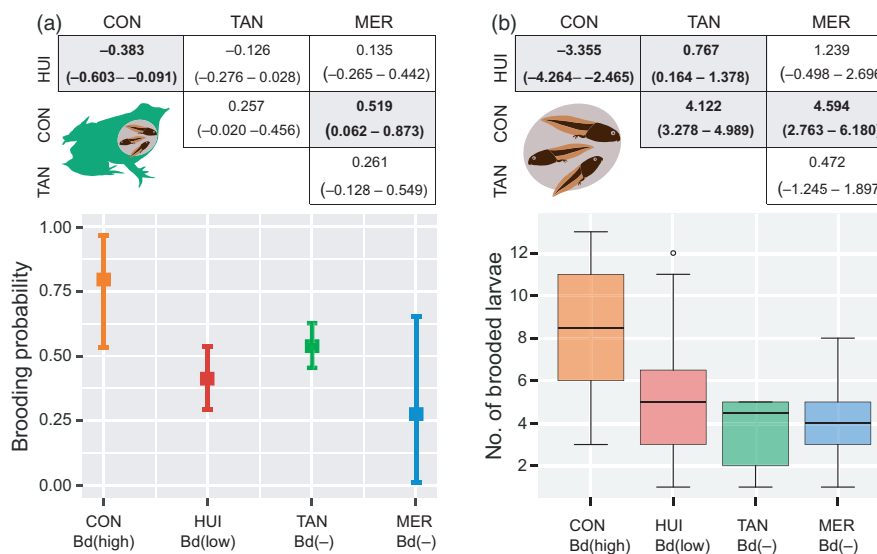


FIGURE 2 Male reproductive effort and in four Southern Darwin's frog *Rhinoderma darwinii* populations from Southern Chile. (a) Annual brooding probability, that is, the probability for a male to be in the brooding state. (b) Number of larvae counted inside the vocal sac of males. We show a pairwise comparison of the mean estimated parameter between the populations (i.e. cell_{*i*} = Ψ row_{*i*} – Ψ column_{*j*}) or Bayesian effect estimates (sensu Kéry, 2010). Effect estimates with Bayesian credible intervals not overlapping the zero are highlighted in bold letters. The error bars in (a) represent the Bayesian credible intervals. In (b), the centre line in each box indicates the median, the upper and lower box sides represent the interquartile range, the whiskers extend to the 5th and 95th percentiles and dots represent outliers

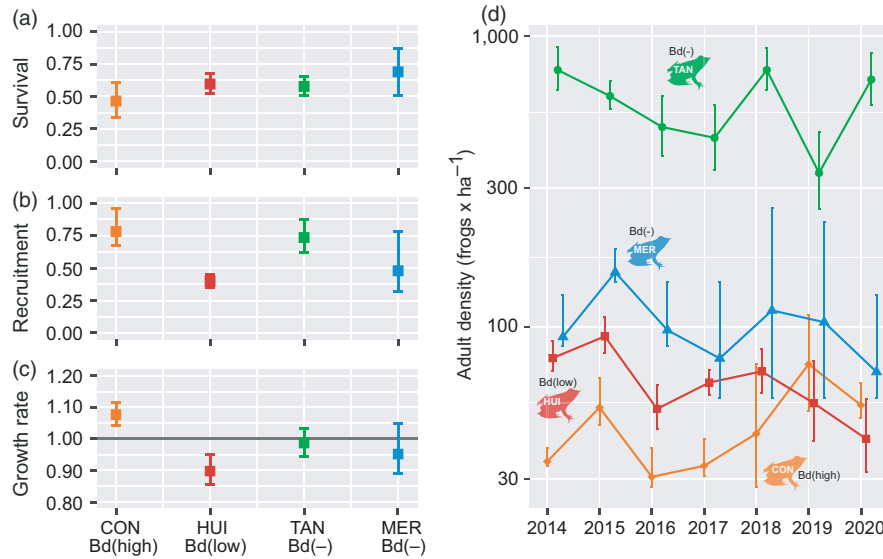


FIGURE 3 Demographic parameters estimated at four Southern Darwin's frog *Rhinoderma darwinii* populations from Southern Chile using capture–recapture data collected between 2014 and 2020. (a) Average annual apparent survival probability of adults. (b) Mean per-capita recruitment. (c) Geometric mean population growth rate. (d) Adult density across the study period. The grey solid line in (c) represents population stability (i.e. growth rate = 1). The parameters were estimated using a Bayesian Jolly–Seber Robust Design capture–recapture model. Error bars represent the Bayesian credible intervals

TABLE 2 Elasticities of the asymptotic population growth rate to changes of vital rates (lower-level elasticities) in four Southern Darwin's frog *Rhinoderma darwinii* populations from Southern Chile. The parameter with the highest potential impact on the asymptotic population growth rate is the one with the highest elasticity. These parameters were estimated using a matrix population model

Parameter	CON – Bd (high)	HUI – Bd (low)	TAN – Bd (–)	MER – Bd (–)
Fecundity	0.371	0.209	0.313	0.269
Survival newborns	0.371	0.209	0.313	0.269
Survival 1-year-old juveniles	0.371	0.209	0.313	0.269
Survival adults	0.258	0.582	0.374	0.462

although the CRIs of this parameter overlapped one [TAN = 0.987 (0.945–1.032); MER = 0.952 (0.891–1.049)]. The only population with strong evidence of decline during this period was the population with a low Bd prevalence [HUI = 0.898 (0.856–0.950); Figure 3c].

3.1.3 | Matrix population model

The elasticity analysis showed that the potential impact on the asymptotic population growth rate of the demographic parameters contributing to adult recruitment (i.e. fecundity, newborn survival and juvenile survival) varied markedly among populations (Table 2). The collective elasticity for these three demographic parameters was highest in the population with high Bd prevalence (CON = 1.113), lower in the Bd-free populations (TAN = 0.939; MER = 0.807) and lowest in the population with a low Bd prevalence (HUI = 0.627). This difference is best illustrated by comparing the ratio between the elasticity of adult survival and juvenile survival, which ranged from 0.70 in the population with high Bd prevalence to 2.79 in the population with low

Bd prevalence. Accordingly, the generation time also varied among populations: it was shortest in the population with high Bd prevalence (CON = 2.7 years), longer in the Bd-free populations (TAN = 3.2 years; MER = 3.7 years) and longest in the population with low Bd prevalence (HUI = 4.8 years).

3.2 | Demographic signal of compensatory recruitment

We found a positive relationship between the proportion of juveniles and *Batrachochytrium dendrobatidis* infection prevalence in the 13 populations surveyed [Bayesian binomial GLM, β coefficient = 0.172 (0.144–0.200); Figure 4]. The proportion of juveniles was high in the three populations with the highest Bd prevalence (some of these populations are separated by more than 440 km; Figure 4). The relationship is almost unchanged when the population with the highest Bd prevalence is removed from the analysis [β coefficient = 0.171 (0.141–0.201)].

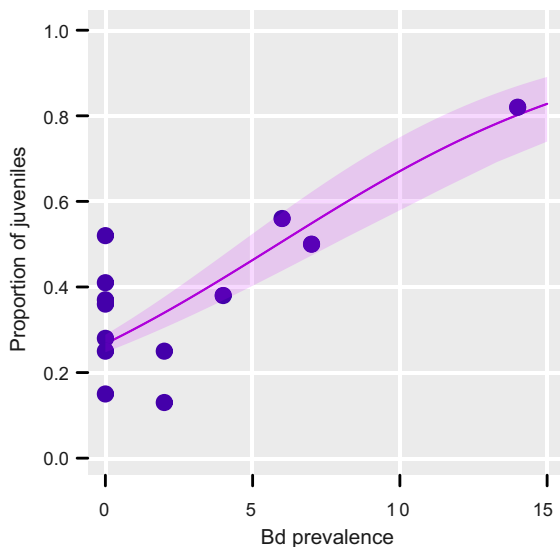


FIGURE 4 Relationship between the proportion of juveniles and *Batrachochytrium dendrobatidis* (Bd) infection prevalence (%) in 13 Southern Darwin's frogs *Rhinoderma darwinii* populations from southern Chile. The purple line represents the predicted relationship from a Bayesian binomial generalized linear model (and the purple area is the Bayesian credible interval). Specifically, in this model, the probability of being a juvenile corresponded to the success probability, and the total number of individuals captured per population corresponded to the trial size, of the binomial distribution

4 | DISCUSSION

Our results indicate that (a) males from the high Bd prevalence population (CON) exhibited the highest reproductive effort among the four *R. darwinii* populations monitored in our 7-year capture-recapture study (Figure 2); (b) this high reproductive effort matched a high adult recruitment, which led to a growing population during the study period despite the high mortality rate in this population (Figure 3); and (c) a positive relationship between the proportion of juveniles and Bd prevalence was detectable in a broad geographical analysis (Figure 4); considering that Bd infection probability and case fatality are similar in adults and juveniles of *R. darwinii*, this pattern suggests a demographic signal of compensatory recruitment in response to Bd infection. This is the first empirical evidence that compensatory recruitment in response to Bd infection can occur through an increase in reproductive effort in amphibian hosts. Here, we discuss plausible explanations for the contrasting life-history strategies observed in the studied *R. darwinii* populations. We also discuss possible mechanisms underlying the putative fecundity compensation observed in our model species. We conclude by discussing the implications of our results for disease mitigation.

4.1 | Interpopulation variation in life-history strategies in *R. darwinii*

Our results highlight that interpopulation variation in demographic rates in *R. darwinii* cannot be attributed to the effects of Bd infection

alone. Indeed, individuals from the high Bd prevalence population, CON, and from the Bd-free population, TAN, exhibited a faster life-history strategy than individuals from the other two populations, including a smaller elasticity of adult survival and a shorter generation time (Table 2). Therefore, the high reproductive effort in males from CON possibly could be attributed, in whole or in part, to a fast life-history strategy present in this population prior to the arrival of Bd, to a high Bd prevalence or a combination of both.

Interpopulation variation in life-history strategies is common in amphibians and has been associated with environmental factors such as climate (Cayuela et al., 2021; Morrison & Hero, 2003) and habitat patch persistence (Cayuela et al., 2016). Seasonality is the environmental factor that shows the strongest variation among *R. darwinii* populations, and this factor correlates with body size variation in this species: individuals from more seasonal areas have a larger body size (Valenzuela-Sánchez et al., 2015). Allometric constraints on life-history traits (Healy et al., 2019) and a positive effect of hibernation on *R. darwinii* survival [see discussion in Valenzuela-Sánchez et al. (2015)] might lead to a faster life-history strategy in populations with a less seasonal climate. This idea partially matches the pattern observed in our study, as individuals from TAN (fast life-history) and HUI (slow life-history) experience, respectively, the least and the most seasonal environments from known *R. darwinii* populations (Valenzuela-Sánchez et al., 2015).

The high Bd prevalence population inhabits an area of moderate seasonality (Valenzuela-Sánchez et al., 2015). Despite long-term monitoring (e.g. Azat et al., 2021; Soto-Azat, Valenzuela-Sánchez, Collen, et al., 2013; Valenzuela-Sánchez et al., 2014, 2015, 2017), we have not noticed any other factor, beyond Bd, that could account for the high mortality rates and high reproductive effort in this population. Even when compared with the other fast-living population (i.e. the Bd-free population, TAN), the per-capita fecundity was five-fold higher in CON (Table S1). It seems most likely that males from this population are responding to the high Bd-induced mortality risk by increasing their reproductive effort; a common host response (see below) referred to as 'fecundity compensation' (Minchella & Loverde, 1981). The existence of fecundity compensation in our model system is also supported by a demographic signal of compensatory recruitment in response to Bd infection in multiple *R. darwinii* populations (Figure 4). It is worth noting that the best evidence to disentangle the contribution of Bd from other drivers of interpopulation life-history variation would be to measure demographic rates before and after Bd arrival to the populations. Unfortunately, as is usual in the amphibian-Bd system (Brannelly et al., 2021), we currently lack data to allow such temporal comparisons in *R. darwinii* populations.

4.2 | Differences in demographic responses among Bd-positive populations

Despite experiencing population decline during the study period, our results suggest that fecundity compensation did not take place

in the population with low Bd prevalence. Individuals from this population exhibited low reproductive effort, which in addition to a less male-biased sex ratio and similar apparent survival probability compared to Bd-free populations, led to the lowest rate of adult recruitment. A lack of fecundity compensation in this population could be associated with an individual's perception of low mortality risk due to low Bd infection risk (Duffield et al., 2017). This hypothesis is supported by the positive correlation between Bd prevalence and the proportion of juveniles across 13 *R. darwinii* populations, which suggest the existence of a prevalence threshold for the occurrence of fecundity compensation in *R. darwinii* populations. A similar positive association between mortality risk and the level of fecundity compensation has been observed in wild boar populations experiencing different levels of harvesting (Servanty et al., 2011).

Life-history strategies can influence host capability to exhibit fecundity compensation (Valenzuela-Sánchez et al., 2021). For instance, at the interspecific scale, empirical evidence shows that slow-living mammals, in contrast to fast-living mammals (e.g. Jones et al., 2008; Servanty et al., 2011), are not able to exhibit fecundity compensation in response to an increased mortality risk (see Servanty et al., 2011 and references therein). Perhaps a naturally lower fecundity rate in the population with low Bd prevalence limited the capability of individuals to exhibit fecundity compensation. Further evaluation of this hypothesis in our model system and elsewhere might provide important insights into the factors shaping compensatory responses of host populations to emerging infectious diseases (Valenzuela-Sánchez et al., 2021). In our study system, a lack of effective fecundity compensation in some *R. darwinii* populations could account for the recently documented extinction of several populations of this species, especially those in undisturbed areas where stressors other than Bd infection are not known to have occurred (Azat et al., 2021; Soto-Azat, Valenzuela-Sánchez, Collen, et al., 2013; Valenzuela-Sánchez et al., 2017).

4.3 | Mechanisms of fecundity compensation

Our results suggest that density-dependent processes did not play a major role in driving the high reproductive effort in the population with high Bd prevalence. Adult density was low and similar in both Bd-positive populations, but male reproductive effort was very different in these populations. The time of arrival of Bd into the Bd-positive *R. darwinii* populations is unknown, but it could have occurred more than 40 years ago (Soto-Azat, Valenzuela-Sánchez, Clarke, et al., 2013; Valenzuela-Sánchez et al., 2018). Thus, rapid evolution in response to Bd infection could have played a role in driving reproductive effort higher (e.g. Bonnet et al., 2017; Stearns et al., 2000). Yet, it is worth noting that rapid evolution is less likely to occur in small, isolated populations, such as those of our study species (Azat et al., 2021), where small effective population size reduces effectiveness of selection against parasites via amplified effects of genetic drift and decreases genetic polymorphism, reducing

the chance of maintaining beneficial alleles via standing genetic variation (Eimes et al., 2011).

A more plausible mechanism underlying fecundity compensation in individuals from the population with high Bd prevalence is phenotypic plasticity triggered by high mortality risk (Stearns, 1989). Empirical evidence shows that parasite-induced plasticity in reproductive traits is common and widespread across the tree of life (e.g. invertebrates, Agnew et al., 2000; vertebrates; Valenzuela-Sánchez et al., 2021; plants, Pagán et al., 2008), including amphibians exposed to Bd (An & Waldman, 2016; Brannelly et al., 2016; Chatfield et al., 2013; Roznik et al., 2015). Since *R. darwinii* individuals die soon after Bd infection (Valenzuela-Sánchez et al., 2017), any increase in reproductive effort in Bd-infected males would play only a minor contribution to the mean reproductive effort in the population. This is analogous to populations of harvested animals exhibiting this kind of compensatory response (e.g. Servanty et al., 2011), that is, fecundity compensation cannot be performed by harvested individuals. We hypothesize that public information, which is used by individuals of a wide range of taxa to assess environmental conditions (Danchin et al., 2004), could signal mortality risk and trigger plasticity in reproductive effort in uninfected individuals of *R. darwinii* (e.g. Toth et al., 2004). Further work should be conducted to disentangle the contribution of the different mechanisms that might underlie the potential fecundity compensation in Bd-positive *R. darwinii* populations. This is of practical importance because evolutionary responses are expected to be more hard-wired and slower to reverse than plastic responses, and can alter population dynamics and resilience to other stressors (e.g. extreme climatic events) even after the additional mortality risk has ceased (Eikeset et al., 2015).

4.4 | Implications for disease mitigation

Our results highlight that population management aimed to mitigate Bd impacts in wild amphibian populations should take into consideration potential interpopulation variation in life histories. For instance, the elasticity analysis is useful to identify potential conservation actions to enable persistence of Bd-positive populations because changes in demographic parameters with high elasticity will produce large changes in the population growth rate (Caswell, 2000). In populations with a fast life history, the best option would be to enhance the demographic parameters contributing to adult recruitment. In our study, since a high reproductive effort and high adult recruitment in CON offset the negative impacts of Bd infection on host survival, a sound option would be to maintain the environmental conditions that enable host-parasite coexistence in this population (Scheele, Foster, et al., 2019; West et al., 2020). Reducing potential non-disease stressors in this population is important because fecundity compensation can be condition dependent and could be reduced in the presence of additional environmental stress (Gleichsner et al., 2016; Roznik et al., 2015). In Bd-positive populations with a slow life history, the best management option

would be to reduce adult mortality. Reducing Bd infection risk, for instance by using exclusionary fences to reduce or halt Bd transmission from reservoir species (Valenzuela-Sánchez et al., 2017), might be a feasible management action to enable population persistence at these populations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.V.-S., C.A. and A.A.C. designed the methodology of the capture-recapture study; A.V.-S. and H.C. conceived the ideas; A.V.-S., C.A., S.D., A.A.C., J.B., J.M.S. and V.T. collected the data; A.V.-S. analysed the data; A.V.-S. led the writing, with contributions from H.C. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data and code used in this study are provided in the Supporting Information or are available at Zenodo <https://doi.org/10.5281/zenodo.5550840> (Valenzuela-Sánchez, 2021).

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SUPPORTING INFORMATION

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