Small body size exacerbates the extinction vortex

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August 11, 2020

Abstract

Understanding the dynamics of small populations is critical to conserve those species at most risk. Previous work has identified demographic and environmental factors that can mutually reinforce one-another to drive populations rapidly to extinction – a process known as the 'extinction vortex.' However, studies investigating robustness to the extinction vortex in relation to life history and ecological traits have been lacking. Here, we assemble a database of 55 vertebrate populations monitored to extirpation and perform three analyses to investigate whether a key fitness-related phenotypic trait – body size – influences the rate at which populations succumb to the extinction vortex. We find evidence that populations of smaller-bodied species deteriorate at a faster rate, suggesting that intrinsic biological traits can alter the susceptibility of species to the extinction vortex, and may serve as a useful feature for prioritizing which populations to invest conservation effort in.

Introduction

The Anthropocene is characterized by an unprecedented rate of biodiversity loss driven by a number of anthropogenic stressors including climate change, pollution, habitat loss, overexploitation and the transmission of invasive species (Young et al. 2016). As populations decline in the face of these stressors the need for conservation intervention becomes increasingly important. However, conserving small populations is complicated as declining population size increases the risk of detrimental demographic processes driving populations inexorably towards extinction (Fagan & Holmes 2006). For example, individual fitness in many species is expected to decrease with population size due to Allee effects (Berec et al. 2007) and a loss of genetic diversity (Saccheri et al. 1998; Blomqvist et al. 2010); demographic stochasticity influences small populations by increasing the annual variability in population growth rate (Fagan & Holmes 2006), which is particularly problematic in small populations as major fluctuations could lead to their extinction (Gilpin & Soulé 1986; Caughley 1994); moreover, small populations are also especially vulnerable to direct extirpation from external drivers of mortality, such as environmental stochasticity and random catastrophes (Caughley 1994). The concurrent presence of these processes is thought to lead to self-reinforcing, rapid and catastrophic downward spirals to extinction, so-called 'extinction vortices' (Gilpin & Soulé 1986), during which there may be little prospect of the population recovering even with intense conservation effort (Palomares et al. 2012). To identify the populations most at-risk and to make informed conservation decisions, we need to understand the factors that determine the robustness of a population to extirpation by the extinction vortex.

Fagan and Holmes (2006) empirically corroborated, albeit with a small database of population extirpations, several preexisting hypotheses of the extinction vortex; specifically, that (i) time to extinction scales to the logarithm of population size, indicating that as a population declines its time to extinction decreases at an increasing rate, (ii) geometric growth rate declines as extinction nears, due to declining individual fitness and (iii) annual variability in population change increases as extinction nears, attributable to an increasing influence of stochastic factors.

A species' intrinsic and ecological traits are often key predictors of extinction risk (Gaston & Blackburn

1995; Purvis et al. 2000; Cardillo et al. 2008), with geographic range size, life-history speed, and degree of specialization emerging as persistent indicators (Chichorro et al. 2019). However, with few exceptions (Duncan & Young 2000; Brashares 2003; Koh et al. 2004), real-life extinctions have rarely been used to infer extinction proneness in relation to biological traits (Brook et al. 2008). Similarly, using a lab-based experiment, Godwin et al. (2020) were the first to explicitly investigate how variation in a specific behavioral trait (mating pattern) can result in differential population vulnerability to the extinction vortex; though analogous studies have not been carried out on real-life population data.

Unfortunately, many of the traits identified as important predictors of extinction risk are difficult to measure, particularly in populations which are already severely reduced, meaning that it is necessary to use proxy measures of these intrinsic ecological traits. Body size is a particularly important trait, associated with a suite of intrinsic, ecological and anthropogenic factors that are frequently invoked in studies relating to extinction risk such as life-history speed (Johnson 2002), population density (Fa & Purvis 1997; Davidson et al. 2009), and the level of exploitation by humans (Owens & Bennett 2000; Ripple et al. 2016, 2019). Furthermore, because of the ease of obtaining body size data and the significance of body size as a correlate of many hard-to-record population traits, it is arguably the most readily available trait available among taxa. This enhances the potential utility in predicting how small populations will respond without having to obtain more cryptic information with time-consuming and expensive data-collection procedures.

Smaller-bodied species are generally more fecund with greater intrinsic rates of growth, meaning they can recover from perturbations more quickly (Brook & Bowman 2005) and spend less time at small population sizes where there is a large threat of extirpation (Allen et al. 2017). However, slower life history speed in larger-bodied species is linked to greater resistance to both environmental (Millar & Hickling 1990; Peltonen & Hanski 1991; Sinclair 2003; Saether et al. 2013; Yeakel et al. 2018) and demographic (Jeppsson & Forslund 2012; Saether et al. 2013) stochasticity. Greater susceptibility to stochastic processes implies that populations of smaller-bodied species can be abruptly reduced to a point where the risk of extinction is acutely high (Schoener et al. 2003; Allen et al. 2017). The relationship between body size and robustness against the extinction vortex thus depends on the relative importance of population growth rate versus susceptibility to stochastic elements.

Here, we assess – for the first time – whether body size can interact with underlying demographic processes to influence the dynamics of a population in the region of an extinction event, building upon the analysis of Fagan and Holmes (2006) but with a much larger database. To do this requires cases of populations monitored through to extirpation, negating the need to designate quasi-extinction thresholds, which could result in erroneous interpretations of extinction dynamics (Fagan & Holmes 2006). We use a global database of vertebrate population time series, supplemented with body size data from various life history databases to identify 55 populations where extirpation has been observed. We find support for the three aforementioned predictions of the extinction vortex (Gilpin & Soule 1986; Fagan & Holmes 2006) and evidence that deterioration in population dynamics, due to the extinction vortex, takes place at a faster rate in smaller-bodied species.

Methods

Population time series data

We obtain populations monitored to extirpation from two sources: i) the Living Planet database (LPD) (http://www.livingplanetindex.org/data_portal), containing annual population abundance data for over 25000 vertebrate populations between 1950-2019 and ii) from previously published work on the extinction vortex (Fagan & Holmes 2006). A diverse range of methods to monitor population abundance are included in the LPD, with the caveat to inclusion in the dataset being that monitoring should be reputable, appropriate for the species and consistent through time. A detailed outline of inclusion criteria for the populations in the LPD are provided by Loh et al. (2005). In some cases, complete censuses of the population were carried out, whereas in others population abundance was monitored using indirect indicators. In the absence of evidence to the contrary, regardless of the method used in population monitoring, we assume that indices of

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population abundance are representative of the true population size at any given point in time.

We define extirpation as a population declining to a zero-abundance count at the end of the time series and identify populations from the LPD that showed this. Zero-abundance counts occurring before the end of the time series might indicate a relatively low species detectability and, correspondingly, a high rate of observation error (Brook et al. 2006). To minimize the possibility of including populations that were not actually extinct and to avoid inflating annual variation in population abundance, we omit time series where zero counts occurred and were followed by subsequent observations. In addition, we only consider populations where the time between the penultimate abundance count and the zero-abundance count (signifying extirpation) was no more than one year, so that we can ascertain the exact year in which the population went extinct. Furthermore, to avoid introducing possible bias from short time series, we only include time series with at least 10 counts of population abundance.

Based on these filtering criteria, we produce a dataset of 55 population extirpations of 52 different species, including two elasmobranchs, five actinopterygians, one amphibian, one reptile, nine mammals and 34 birds. Our dataset of time series has a mean length of 15.98 ($\pm$6.65) years.

Life history data

We compile life history data for all species in this dataset from various life history databases (Myhrvold et al. 2015; Oliveira et al. 2017; Froese & Pauly 2000), extracting data on log-transformed (base 10) adult body mass in kg. Additionally, where possible, we collate up to six other traits indicative of life history speed: maximum longevity, female maturity, incubation time, fledgling age, number of litters per year and litter/clutch size. We log-transform (base 10) these trait values and investigate their relationship with body mass using linear models.

LMM/GLMMs

We perform all statistical analyses using R version 3.6.1 (R Core Team, 2019). We perform three statistical analyses to investigate how population dynamics change in the region of an extinction event. For each analysis we use linear or generalized linear mixed effects models (LMMs/GLMMs) in the 'nlme' (Pinheiro et al. 2019) and 'glmmTMB' (Brooks et al. 2017) packages respectively, to account for context-specific factors that could mask the effect size of fixed effects on the response variables. We account for the nested random effects of our data using a mixed modelling framework, with population nested inside species, nested inside units, nested inside data type. This accounts for the site-specific effects on the population dynamics, the potential effects of relatedness at the species level and the potential effects of units of measurement. These are nested within data type, which is consistent across species and populations, but may vary between species and units. We present full descriptions of the fixed and nested random effects used in our LMMs/GLMMs in Table 1. We also normalize our fixed effects to enable easier comparison of the relative importance of each variable in the models. As avian taxa are overwhelmingly represented in the dataset (65.38% of species), we perform our analyses on all populations together, as well as two subsets: i) only avian populations and ii) only non-avian populations. For each analysis, we employ AIC-based model selection to identify the best fitting model using the 'MuMIn' package (Bartón 2019).

Years to extinction

Firstly, we assess how proximity to extinction changed as a function of population size and the body size of the species. To make each time series compatible in the same analyses, we convert time to count backwards from extinction to produce a new variable ('years to extinction') with a consistent meaning across all populations. For an extinction vortex to be present, time to extinction is expected to change as a function of the logarithm of population size. To test this, and simultaneously the influence of body mass (BM), we fit GLMMs with the structures *years to extinction ~ population size + $log_{10}(BM)$ + population size:$log_{10}(BM)$* and *years to extinction ~ $log_{10}(population size)$ + $log_{10}(BM)$ + $log_{10}(population size)$:$log_{10}(BM)$* , including a first-order autoregressive error structure to account for time series autocorrelation. Following Fagan and Holmes (2006), we exclude the final abundance count from each time series. We attempted to fit these models with a negative

binomial error distribution, however none of the models would converge. We therefore fit a Poisson error distribution and test the models for overdispersion using the 'DHARMa' (Hartig 2020) package.

Geometric growth rate

According to the extinction vortex, as a consequence of declining individual fitness due to genetic deterioration and Allee effects, the year-to-year rate of population change (geometric growth rate) is expected to become increasingly negative as population size diminishes. We calculate geometric growth rate (λ) as: λ = ln (N_t / N_{t+1}), where N_t is the population abundance in a given year and N_{t+1} is the population size one year further away from extinction. To permit finite estimates of a populations' final growth rate before extirpation, we add a constant [1] to each population abundance measurement. We were not able to calculate geometric growth rate in years where there were gaps of more than one year until the next abundance count. We fit LMMs with the structure λ ˜ *log10(population size) + log_{10}(BM) + log10(population size):log_{10}(BM)* . A positive coefficient for population size in these models would support the hypothesis that per capita growth rate decreases with population size.

Detrended variability

As populations decline, the influence of stochasticity is expected to increase and contribute to their extinction. This should manifest itself in greater annual variability in population change at closer proximity to extinction. To investigate this, we extract the residuals from models of the structure λ ˜ $\psi\epsilon\alpha\rho\varsigma$ τo $\epsilon\xi\tau\iota\nu\varsigma\tau\iota o\nu$ and square them to remove the trend. We then natural log-transform these squared residuals for normality. Therefore, these values represent the logged, detrended annual variability [$ln(residuals)^2$] in population growth rate. We fit LMMs with the structure*[ln(residuals^2)] ˜ years to extinction + log_{10}(BM) + years to extinction:log_{10}(BM).* Support for the hypothesis that variability in annual population growth rate increases as extinction draws nearer in time would be found by a negative relationship with years to extinction in these models.

For each analysis, we present a ranking of the best fitting models in Table 2. We present a full summary of the best fitting models in the Supporting Information (see Table S1 in Supporting Information).

Results

Relationship between body size and life history traits

We found a significant positive relationship between body mass and maximum longevity, female maturity, incubation time and fledgling age, and a significant negative relationship between body mass and litter/clutch size (Fig. S1). This suggests that body size in our species represents a useful umbrella trait which captures information on their life histories, and thus is a trait which could influence the rate of population declines due to the extinction vortex.

GLMM/LMMs

Years to extinction

In agreement with the first hypothesis, models with a log-transformed population size significantly outperformed those fit with non-logged population size (Δ AIC > 2) for data on all species combined, only birds and only non-avian species (Table S2). Also, in all three groups of data a positive interaction between body size and population size was included in a model within two AIC units of the best fitting model (Table 2); these models suggest that populations of smaller-bodied species are under imminent risk of extinction over a larger range of population size.

Geometric growth rate

In all three groups, we found a significant positive relationship between geometric growth rate and log-transformed population size (Table 2; Fig. 1). The clear best performing models included a significant negative interaction between population size and body mass in all three sets of data (Table 2; Fig. 1), indicating that the rate at which a population deteriorates is faster in smaller-bodied taxa.

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Population variability

For all three groups, we found a significant negative relationship between the log-transformed detrended variability in population change and years to extinction (Table 2; Fig. 2), showing that year-to-year population variability does indeed increase as extinction is approached. In relation to body size, all our models suggest that the magnitude of annual population variability is higher as body size decreases (Table 2; Fig. 2). An interaction between body size and years to extinction was included in the best fitting models, or those within two AIC units thereof (Table 2). This interaction was significant and negative in the non-avian subset (Table 2), suggesting a greater increase in variability in larger-bodied taxa.

Discussion

Understanding the dynamics of small populations is critical for the effective conservation of at-risk species. Previous work has demonstrated an increase in extinction proneness in declining populations (Fagan & Holmes 2006). Here, we corroborate preexisting theoretical and empirical studies on the extinction dynamics of populations and, additionally, show for the first time that the rate of the extinction vortex can be altered by body size.

Reinforcing previous findings, our results show that the proximity of a population to extinction is dependent on the logarithm of population size (Lande 1993; Fagan & Holmes 2006). This suggests that the proximity to extinction decreases at an increasing rate as a population declines, indicative of an extinction vortex. Accordingly, care should be taken to maintain populations at high densities to avoid self-reinforcing spirals to extinction and to maximize the probability of long-term persistence (Fagan & Holmes 2006). We cannot rule out the influence of body size; the best fitting models did not provide a significantly improved fit compared to those that included an interaction term between body size and population size (Table 2). The positive coefficients for the interaction between populations size and body size (Table 2), suggests population size becomes increasingly important in determining the distance from extinction as body size increases. As such, smaller-bodied species appear to be more vulnerable to imminent extinction across a greater range of population sizes, in agreement with previous studies reporting greater population persistence among species with slower life history traits (Newmark 1995; Saether et al. 2005). Our relatively small dataset may account for the fact that this is not the clear best performing model in this analysis.

According to the extinction vortex, genetic deterioration and Allee effects are expected to result in proportionally larger declines as population size diminishes (Brook et al. 2008). Indeed, we found an increase in the year-to-year per capita rate of decline as population shrinks (Table 2; Fig. 1). The implication of this is that even with conservation intervention, species that fall into the extinction vortex may struggle to be saved and require a non-linear increase in the magnitude of the change required to save a population as it moves towards extinction. Well-studied populations on the verge of extirpation support this; the decline of the Florida panther population (*Puma concolor coryi*) was only reversed after the introduction of several individuals translocated from healthy populations leading to the restoration of genetic diversity (Johnson et al. 2010). In practical terms, this emphasizes the need for early conservation intervention, with a strong focus on ensuring species do not fall into the extinction vortex.

Our results suggest that the key question of when a species is at risk of rapidly collapsing to extinction is not only a function of population size, but is also affected by the body size of the species; we found evidence that small body size exacerbates the rate of decline in geometric growth rate as population size declines (Fig. 1). This was true for all groups (Table 2), suggesting a similar trend across the vertebrate phylum. Though it is acknowledged that extinction risk is an emergent property of the interaction between biological traits and the type of threatening process (Owens & Bennett 2000; Isaac & Cowlishaw 2004; Price & Gittleman 2007; Brook et al. 2008; Davidson et al. 2009; Ripple et al. 2017), our findings may seem at odds with the frequently reported positive association between body size and extinction threat level (e.g. IUCN threat status) (Gaston & Blackburn 1995; Bennett & Owens 1997; Cardillo et al. 2005; Liow et al. 2008; Dirzo et al. 2014). However, the extinction risk of highly fecund species is tempered by naturally larger populations (Tracy & George 1992; Newmark 1995); species at the fast end of the life history speed continuum seem to be

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more vulnerable after controlling for the confounding effect of population size (Cook & Hanski 1995; Johst & Brandl 1997; Saether et al. 2005; Hilbers et al. 2016). A possible explanation is that smaller-bodied species have faster life histories and are more susceptible to stochastic elements (Peltonen & Hanski 2001; Sinclair 2003; Saether & Engen 2002; Saether et al. 2004; Wilson & Martin 2012), therefore they are predisposed to respond faster to the deleterious demographic impacts of genetic decay, Allee effects and other stressors.

The results of our third analysis, investigating population variability through time, supports the idea that stochastic processes are involved in causing the extirpation of these populations (Fagan & Holmes 2006; Brook *et al* . 2008). That the magnitude of annual population variability is higher in smaller-bodied species is indicative of lower population stability in smaller-bodied species, as has been noted elsewhere (Sinclair 2003). This may also help to explain the significant negative interaction between body size and years to extinction in the non-avian subset (Table 2); given that the population dynamics of smaller-bodied species is inherently more stochastic, any increase in year-to-year variability due to stochastic elements could be less detectable. We suspect that a similar pattern is not observed in our avian subset because of the small variation in body size; the range of body masses in our avian subset (~7kg) is two orders of magnitude smaller than that of our non-avian subset (~350kg).

In conclusion, despite the large disparity in ecological and environmental contexts among populations constituting this study, we find evidence that small body size exacerbates the rate of the extinction vortex, providing one of the first studies to investigate differential vulnerability to the extinction vortex in relation to intrinsic biological traits and, to our knowledge, the first to specifically investigate this in real-life populations. The practical relevance of our findings is highlighted by the fact that species-specific data on body size is arguably the most widely available across all taxa, and our results demonstrate the need for a generally conservative approach to population targets especially in small-bodied taxa with fast life history speeds and a high susceptibility to stochastic processes.

Acknowledgments

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Figure Legends

Figure 1. a) The coefficient estimates of the best fitting models from the second analysis (*geometric growth rate*). Circles and bars show estimates and 95% CIs, respectively. The fixed effects were standardized (mean = 0, standard deviation = 1) prior to modeling, therefore the intercept shows the distribution of modeled geometric growth rate with mean values for population size and body mass. Also, coefficient estimates show the expected change in years to extinction given a one standard deviation increase in each fixed effect. Where CIs for a fixed effect do not overlap with zero demonstrates a positive or negative effect for that fixed effect, otherwise there is a mixture of positive and negative effects. Also, interaction plots are presented for b) all species, c) avian species and d) non-avian species. Error bars indicate 95% CIs.

Figure 2. a) The coefficient estimates of the best fitting models from the third analysis (*population variability*). Circles and bars show estimates and 95% CIs, respectively. The fixed effects were standardized (mean = 0, standard deviation = 1) prior to modeling, therefore the intercept shows the distribution of modeled annual population variability with mean values for population size and body mass. Also, coefficient estimates show the expected change in years to extinction given a one standard deviation increase in each fixed effect. Where CIs for a fixed effect do not overlap with zero demonstrates a positive or negative effect for that fixed effect, otherwise there is a mixture of positive and negative effects. Also, interaction plots are presented for b) all species, c) avian species and d) non-avian species. Error bars indicate 95% CIs.

Figures

Fig. 1.

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Fig. 2.

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Tables

Table 1. Outline of parameters used in LMMs/GLMMs.	**Table 1.** Outline of parameters used in LMMs/GLMMs.
Parameter	**Description**
Population ID	Unique ID from the LPD representing a single population. acco
Species name Units Data type	Species binomial accounting for species-specific effects. The unit
Population size	Raw population abundance measurement taken from the LPD.

Table 1. Outline of parameters used in LMMs/GLMMs. **Table 1.** Outline of parameters used in LMMs/GLMMs.

Log_{10} Population size	Log-transformed (base 10) population abundance measurement.
Body mass (BM)	Log-transformed (base 10) body mass (kg) of species.
Years to extinction	Rescaled time variable, counting backwards from extirpation