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LETTER

Quantifying the extinction vortex

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Abstract

We developed a database of 10 wild vertebrate populations whose declines to extinction were monitored over at least 12 years. We quantitatively characterized the final declines of these well-monitored populations and tested key theoretical predictions about the process of extinction, obtaining two primary results. First, we found evidence of logarithmic scaling of time-to-extinction as a function of population size for each of the 10 populations. Second, two lines of evidence suggested that these extinction-bound populations collectively exhibited dynamics akin to those theoretically proposed to occur in extinction vortices. Specifically, retrospective analyses suggested that a population size of *n* individuals within a decade of extinction was somehow less valuable to persistence than the same population size was earlier. Likewise, both year-to-year rates of decline and year-to-year variability increased as the time-to-extinction decreased. Together, these results provide key empirical insights into extinction dynamics, an important topic that has received extensive theoretical attention.

Keywords

Decline to extinction, extinction risk, extinction vortex, population extinction, time-to-extinction, vertebrate extinctions.

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INTRODUCTION

In coining the term 'extinction vortex', Gilpin & Soulé (1986) argued that as populations decline, an insidious mutual reinforcement can occur among biotic and abiotic processes such as environmental stochasticity, demographic stochasticity, inbreeding, and behavioural failures, driving population size downward to extinction. In the two decades since that work, extinction-related issues have continued to motivate research by ecologists and conservation biologists, leading to the development of population viability analyses and related approaches where the aim is to characterize the risk of extinction that particular populations face (Morris & Doak 2003). In contrast to the large body of research, especially by theoreticians, that has focused on risks of extinction, far fewer studies have investigated the dynamics of actual extinction events. Studies by Belovsky *et al.* (1999) on laboratory populations and by Schoener *et al.* (2003) on island invertebrates are among the rare exceptions that have provided much needed empirical perspectives on the dynamics of extinction.

For vertebrate populations, ecologists' understanding of extinction dynamics is far less clear. Indeed, even though ecologists can cite a plethora of empirical examples of situations in which species with previously robust populations have declined in numbers or spatial distribution (e.g. Kunin & Gaston 1997, Akçakaya 2004), quantitative data on the dynamics leading up to actual extinction events in vertebrate populations remain rare. Instead, almost all quantitative analyses of population-level extinction dynamics for vertebrates are either wholly theoretical or tied to populations that may have declined but have not gone extinct (e.g. Tuljapurkar 1990; Dennis *et al.* 1991; Ludwig 1999; Brook *et al.* 2000; Ripa & Lundberg 2000; Holmes & Fagan 2002; Lande *et al.* 2003). In those few cases where ecologists have actually witnessed extinction events in vertebrate populations, available data tend to afford only short or highly patchy time series, neither of which permits detailed quantitative investigation of a population's dynamics as it declines to extinction.

To address the critical need for a multispecies summary of the dynamics by which well-monitored vertebrate populations decline to extinction, we combed published and unpublished sources to develop a small database with which we could quantitatively characterize the final declines of wild vertebrate populations. We were also interested in using the collected time series to test two primary theoretical predictions about the process of extinction. The first prediction was that, for populations that go extinct, population lifetimes should scale logarithmically with population size. Some version of this prediction emerges consistently from a wide variety of deterministic and stochastic population models, including some that incorporate density-dependence (Lande *et al.* 2003). For example, this prediction is found in models where populations start at their carrying capacity (Lande 1993) or below their carrying capacity (Engen & Saether 2000), regardless of whether the models incorporate a deterministic, exponential decay or demographic or environmental stochasticity. Indeed, if a population's long-run growth rate is negative, then density-independent models will predict logarithmic scaling of population lifetimes. In addition, under conditions of environmental stochasticity, population lifetimes will scale logarithmically with starting population size even if the long-run population growth rate is not negative (Lande 1993; Lande *et al.* 2003). Time series of populations monitored to extinction afford a unique opportunity to test this key prediction about extinction dynamics.

The second core prediction emerges from Gilpin & Soulé (1986) conceptualization of the extinction vortex (see also Tanaka 2000; Dennis 2002). In particular, the vortex framework suggests that key aspects of a population's dynamics should deteriorate as extinction nears because population declines are likely to beget further declines and because stochastic factors assume increased importance at small population size. For example, positive feedbacks are hypothesized to occur among population declines, demographic and environmental stochasticity, and loss of genetic diversity, accelerating a population's collapse (Gilpin & Soulé 1986). In current usage, some discussions of extinction vortex dynamics focus almost exclusively on genetic issues (McGinnity *et al.* 2003), but the initial formulation of the vortex concept emphasized mutual reinforcement among a diversity of factors that collectively cause the population dynamics of small populations to deteriorate (Gilpin & Soulé 1986). Put quantitatively, such deterioration of population dynamics could include such features as proportionately larger declines in abundance as a population nears extinction and an increase in interannual variability in changes in population size at smaller population sizes because of stochastic effects. In this paper, we use time series data to test these and related predictions concerning the deterioration of population dynamics in extinction-bound populations.

METHODS

We have been researching the population dynamics of species of conservation concern for a number of years using empirical time series data (Holmes & Fagan 2002; Holmes *et al.* 2005; E.E. Holmes and W.F. Fagan, unpublished manuscript). To this end, we have developed a database of such time series using a variety of extensive searches. For example, we have (1) searched all published status reviews, biological opinions, and listing announcements for proposed and listed species in the USA, UK, Australia, New Zealand, and to a limited degree, continental Europe and Africa (although data from those later areas is less available); (2) researched the IUCN Red List to identify species with high quality time series data; (3) personally contacted dozens of government and academic scientists working on species of conservation concern; (4) conducted an extensive search of the published literature available online; (5) physically searched natural history journals not covered by online databases; (6) searched the Global Population Dynamics Database; (7) searched databases maintained by National Marine Fisheries Service and the National Marine Mammal Laboratory; and (8) utilized personal contacts with conservation biologists through our other research and professional collaborations.

Through these efforts, we found 10 time series from annual monitoring programmes, each at least 12 years long, which quantified how a wild vertebrate population (or closed sub-population) declined to extinction. Two mammal populations, five bird populations, two turtle populations, and one fish population comprised our sample. During our search, we encountered many cases where populations or species were presumed extinct but where annual monitoring had not occurred (e.g. Dulvy *et al.* 2003). We also found a few other examples of populations monitored to extinction that we excluded on the basis of time series length [e.g. house sparrows (*Passer domesticus*) in Lande *et al.* 2003] or fragmentary knowledge [e.g. heath hen (*Tympanuchus cupido cupido*) in Simberloff 1988]. We also excluded the many 'bird-on-island' studies where tiny 'populations' of birds (usually one to five pairs) were monitored through to extinction, often followed soon thereafter by recolonizations (e.g. Diamond 1988; Pimm *et al.* 1988).

In all multispecies (but not single species) analyses discussed below, we opted to exclude the one fish population [a population of coho salmon (*Oncorhynchus kisutch*)] because the salmon time series differed from those of the other nine populations in several important ways. First, because adult salmon die after spawning, none of the individuals counted 1 year occurred in subsequent censuses. This is not the case for the terrestrial populations where considerable overlap existed among individuals across years. Second, this 'monocarpic' life history coupled with a development time of *c.* 3 years for coho also leads salmon biologists to standardize their data as 3-year running sums rather than direct population counts, which induces a different type of autocorrelation structure in the salmon time series than in the terrestrial vertebrate time series. Third, the salmon population started its decline from a population size two orders of magnitude higher than the other populations, which introduced significant heteroschedasticity into multi-species analyses that could not be overcome by any of the common statistical transformations.

We also point out that our data set is biased because (1) we are specifically considering populations that actually went extinct; and (2) all of the time series that led to extinctions were 12–21 years long. The first bias is important because it means we cannot address issues of how extinction risk depends on population size in general, but rather must restrict our attention to the dynamics of actual extinction events. The second bias limits our interpretations of calculated risk metrics (e.g. median time to extinction) because we were more likely to encounter time series that went extinct after a few years than after many years. In developing our database of real extinction events, we have also accumulated a substantial data set of time series of long-term enumerative censuses (i.e. not just density estimates) for vertebrate populations, which have been (and continue to be) analysed to understand the dynamics of stochastic population time series and quasi-extinction dynamics (Holmes & Fagan 2002; Holmes *et al.* 2005, E.E. Holmes and W.F. Fagan, unpublished data). In the course of this other research, it became apparent that the dynamics of actual extinction events were different than 'quasi-extinction' (in which a population declines to a threshold above actual extinction), even when that threshold was quite small. That dynamics of the final collapse to extinction might be different than the dynamics of decline to critical quasi-extinction thresholds is not surprising. However, by considering the actual extinction events separately, we seek to quantify such changing dynamics. In developing our database, we believe we have exhausted all conventional and many unconventional approaches to data-mining for vertebrate populations monitored through to extinction. Because of the inherent biases in our data set, we emphasize that our overarching goal is to understand the dynamics of actual extinction events rather than to understand how small population size is associated with extinction risk.

We first made a simple quantitative description of our collection of declines to extinction. We calculated from each time series a variety of relevant metrics. These included: (1) the smallest population size from which an increase in numbers occurred; (2) the population size at which the final decline to extinction (uninterrupted by any increases in population) began; and (3) the population size 1 year before extinction. Populations were deemed extinct when they declined to one or zero individuals. Some of the analyses described below involved calculating year-to-year population growth (decline) rates as $\ln(N_{t+1}/N_t)$ where N_t is the population size at time t. For the last year-to-year transition, we used $N_{\mathrm{Final}} = 1$ for all time series so that we could obtain finite estimates of each population's final decline (i.e. if we did not do this we would have $\ln(0/N_{\mathrm{Final\text{-}1}}) = -\infty$). For plotting and analyses, we rescaled time in each time series to count backwards from extinction. We denoted time-to-extinction as τ where a population is extinct at time $\tau = 0$, the year immediately before extinction is $\tau = 1$, etc. This transformation of time to time-to-extinction provides a common origin with consistent meaning for all time series. Note also that in this framework, year-to-year population growth (decline) rates are calculated as $\ln(N_\tau/N_{\tau+1})$.

As discussed in the Introduction, we sought to use the database of collected extinctions to evaluate two core predictions emerging from theoretical models of population dynamics. The first of these was that, for populations declining to extinction, time-to-extinction should scale logarithmically with population size (Lande 1993; Lande *et al.* 2003). To test statistically for such logarithmic scaling in the collection of nine terrestrial vertebrate time series as a group, we used multilevel mixed regression (Hedeker & Gibbons 1996), also known as hierarchical linear regression (Bryk & Raudenbush 1992). In this technique, individual censuses (called level-1 observations) are nested within populations (called level-2 observations) and a repeated measures random effects model is used to represent differences among populations. We fit models that used an autoregressive [AR(1)] error structure for the autocorrelation within time series and restricted our analyses to non-zero censuses to avoid biasing the fit. In multilevel mixed regression, marginal maximum likelihood, rather than least squares, is used to estimate one set of regression parameters for the data set as a whole and also to obtain empirical Bayes estimates of the regression slope for each population. We used multilevel mixed regression to compare the relative performance of two regression models, one that fit a linear relationship between time-to-extinction and population size and one that fit a logarithmic relationship between those variables. Because the two models had the same number of parameters, we could compare the significance of the difference between the models using AIC (Hilborn & Mangel 1997). We also conducted a separate analysis by fitting linear and logarithmic regressions to the collection of initial population censuses, one from each of the nine terrestrial time series. This method reduced our power to detect a significant slope (each time series only contributed one data point), but was useful because it allowed a separate estimate of logarithmic scaling of time-to-extinction on population size across time series.

The second prediction, we sought to evaluate was whether aspects of each population's dynamics deteriorated as extinction neared. We explored this issue in three ways, each of which afforded different perspectives on extinction vortex dynamics. All three of these approaches are 'retrospective' in the sense that they can only be conducted for populations that actually decline to extinction (though of course one could conduct parallel analyses substituting some quasi-extinction threshold for actual extinction). We detail our three methods in the paragraphs that follow and merely outline our analyses here. First, we tested whether, across populations, year-to-year rates of decline increased as extinction neared. Second, we tested whether, across populations, year-to-year rates of decline became more variable as extinction neared. Third, we asked whether the 'value' of a particular population size (in terms of the time-to-extinction it afforded) decreased as extinction neared. Each of the three analyses makes different assumptions and has different potential drawbacks, but collectively they provide an overview of how populations' dynamics change as extinction nears.

Method 1

For the set of nine terrestrial time series (148 non-zero censuses), we used multilevel mixed regression to test the hypothesis that $\ln(N_\tau/N_{\tau+1})$ depended significantly on τ. We also tested this hypothesis separately for the salmon time series using linear regression. A positive slope in these regressions indicates that population declines nearer to extinction are larger than those in the preceding years. For comparison purposes, we also used multilevel mixed regression to test the related hypothesis that $\ln(N_\tau/N_{\tau+1})$ depended significantly on $N_{\tau+1}$.

Method 2

We next used multilevel mixed regression to test the hypothesis that changes in population size became more variable as populations approached extinction. We conducted this analysis for the set of nine terrestrial time series, but also tested this hypothesis separately for the salmon time series using linear regression. In both cases, we quantified variability as the square of the residuals from the regressions in method 1 (thus, we considered detrended variability, not variability *per se*). A negative slope indicates more variable dynamics in the years immediately preceding extinction. For comparison purposes, we also used multilevel mixed regression to test the related hypothesis that changes in population size became more variable at low population size.

Method 3

For the nine terrestrial populations, we used multilevel mixed regression to test the significance of time period ($\tau \leq 9$ vs. $\tau \geq 10$) as a categorical predictor variable. This analysis provides a perspective on how the relative 'value' of a particular population size may change as a function of time-to-extinction. The multilevel structure of the analysis accounts for the fact that the nine time series contribute differentially to the two time periods, allowing us to test the hypothesis that a logarithmic regression fit to the subset of datapoints 10 or more years from extinction is significantly different than a logarithmic regression fit to the subset of datapoints nine or fewer years from extinction.

There are certain intuitive 'cross-validation' analyses that we did not do. For instance, we did not calculate the predicted probabilities of extinction (e.g. Dennis *et al.* 1991; Holmes 2004) using, say, the first 5–10-year data in each time series to assess how well we could have predicted the actual extinction events. For our purposes, however, such analyses are non-sensical, in that our sample only includes the time series that did in fact go extinct. To see this, consider a situation in which the true probability of extinction for a set of populations is low. In this case, some time series will nonetheless go extinct. By focusing only on that subset of populations that do go extinct, we cannot address the question of extinction probabilities overall (because we do not see the time series where the populations persist). Instead, cross-validation analyses and related questions concerning bias and precision in estimated extinction risk metrics must be addressed using a database of time series that did and did not go extinct, as we have done elsewhere (Holmes & Fagan 2002; Holmes *et al.* 2005, E.E. Holmes and W.F. Fagan, unpublished data). Moreover, we would like to point out that calculating probabilities of extinction for quasi-extinction using 5–10-year data are imprudent. The imprecision in such estimates increased dramatically if *c.* < 15-year data are used for estimation.

RESULTS

For four of the 10 extinction-bound populations, increases in abundance were never observed once the populations dropped below 50 individuals (Table 1). In contrast, for two other populations, increases in abundance were observed even with fewer than 10 individuals, but these increases were short-lived. On average (± 1 SE), final declines to extinction (uninterrupted by even a single year-to-year increase in population size) started from 70 (± 39) individuals [this drops to 49 (± 17) individuals when we exclude the salmon population], but three populations declined directly from > 100 individuals (Table 1). The rate at which a population declined directly to extinction from its final population peak did not depend significantly on how large the population was when it began its final descent (regression, N.S.). Interestingly, for two of the populations (red-cockaded woodpecker and wood turtle B), the year-to-year declines from the final peaks were sufficiently variable so that the overall trend in $\ln(N_\tau/N_{\tau+1})$ was statistically indistinguishable from 1.0 – even though during these declines the populations never exhibited a year in which population size increased relative to the previous year. Averaged across the 10 populations, the final census before

Table 1 Quantitative summary of 10 vertebrate time series in which populations were monitored to extinction

Species	References	Monitoring period (years)*	Smallest population size from which an increase occurred	Population size at which final decline began	Final population size before extinction†	Coefficient of logarithmic decline [years/ln(individuals)]‡
African wild dogs¶	Ginsberg *et al.* (1995)	20	12**	26	26	9.17
Vancouver Island marmots	Bryant (1998); http://www.marmot.org	21	2	3	3	9.26
Middle spotted woodpecker¶	Pettersson 1985	16	5	7	7	9.26
Red-cockaded woodpecker	Baker (1983)	14	16	19	10	8.47
Golden plover	Parr (1992)	18	85	112	7	7.04
Whooping crane	T. Stehn, US Fish and Wildlife Service, personal communication	16	3	6	2	9.26
Hawaiian crow	US Fish and Wildlife Service (2003)	12	12††	12††	2	9.17
Wood turtle A	Garber & Burger (1995)	19	29	31	6	8.55
Wood turtle B	Garber & Burger (1995)	19	53	58	8	8.13
Snake River coho‡‡	National Marine Fisheries Service (1996)	20	233	404	6	2.34

*Monitoring period includes year in which extinction occurred

†Population deemed extinct when census indicated ≤ 1 individual remaining.

‡Calculated from multilevel mixed regression with AR(1) autocorrelated error; for terrestrial species only; see Fig. 1.
Residual^2 calculated from regression of $N_\tau/N_{\tau+1}$ on N_τ (the preceding column).

¶Missing population estimate for one census was interpolated.

**Increased three times from this population size.

††Population never increased during period covered by the time series.

‡‡Population size recorded as three year running sums.

extinction was eight (± 2) individuals, but this ranged from 2 to 26 individuals (Table 1).

For the nine terrestrial populations as a group, time-to-extinction scaled logarithmically as a function of population size (Fig. 1a), confirming our first major prediction. We found time-to-extinction to be significantly related to both population size and log (population size) by separate analyses using multilevel mixed regression ($P < 0.001$ in each case). However, when we fit a multispecies regression model involving log (population size) we obtained $\tau = -15.9 + 9.1 \times \log(N_\tau)$, which offered a significantly improved fit compared with the model including a linear decline (Δ log-likelihood = 470, $P < 0.0001$). The negative intercept in the regression model, which was a fitted parameter, allows for the fact that, across populations, population sizes were somewhat larger than zero immediately before extinction. The multilevel mixed regressions also yielded empirical Bayes estimates of the logarithmic scaling slopes for each of the terrestrial time series (Fig. 1b,c); these regression slopes are given in Table 1. We note that a power-law model [$\log \tau = -1.53 + .81 \times \log(N_\tau)$] also fit the multispecies dataset well [Δ log-likelihood = −1.8 (relative to the logarithmic fit)], but we know of no theory that would suggest such a relationship should be preferred over a logarithmic scaling form.

For the analysis of time-to-extinction using only the nine initial population sizes (i.e. one point from each of the terrestrial time series), an ordinary logarithmic regression was significant ($r^2 = 0.61$; $P < 0.01$; Fig. 1a) and represented a significant improvement over the corresponding linear fit ($r^2 = 0.46$). For salmon, log (population size) performed marginally better than population size as a predictor of time to extinction (Fig. 2a).

For the second major prediction, that the dynamics of populations should deteriorate as they near extinction, we break the results into three parts, corresponding to the three methods outlined above. First, multilevel mixed regression indicated that for the nine terrestrial populations as a group, year-to-year population declines nearer to extinction were larger [i.e. $\ln(N_\tau/N_{\tau+1})$ was more negative] than those in earlier years (Fig. 3). The fitted multispecies regression model was $\ln(N_\tau/N_{\tau+1}) = -0.50 + 0.034 \times \tau$ ($P < 0.0001$). In the comparison model where we used population size rather than time-to-extinction as a predictor variable, the fitted multispecies regression model was $\ln(N_\tau/N_{\tau+1}) = -0.32 + 0.004 \times N_\tau$ ($P = 0.06$), which indicates that year-to-year declines also tended to be larger for smaller population sizes. However, the model involving time-to-extinction afforded the better fit (Δ log-likelihood = 12.7, $P < 0.005$). Inspection of Fig. 3 suggests that each population's final drop to extinction might be having an undue influence on the signal of declining conditions nearer to extinction. However, excluding the final year-to-year transition of each population (i.e. using data only for $\tau \geq 2$), we found that the fitted multispecies regression model was still significant [$\ln(N_\tau/N_{\tau+1}) = -0.22 + 0.011 \times \tau$ ($P < 0.03$)]. This result indicates that the populations' dynamics were

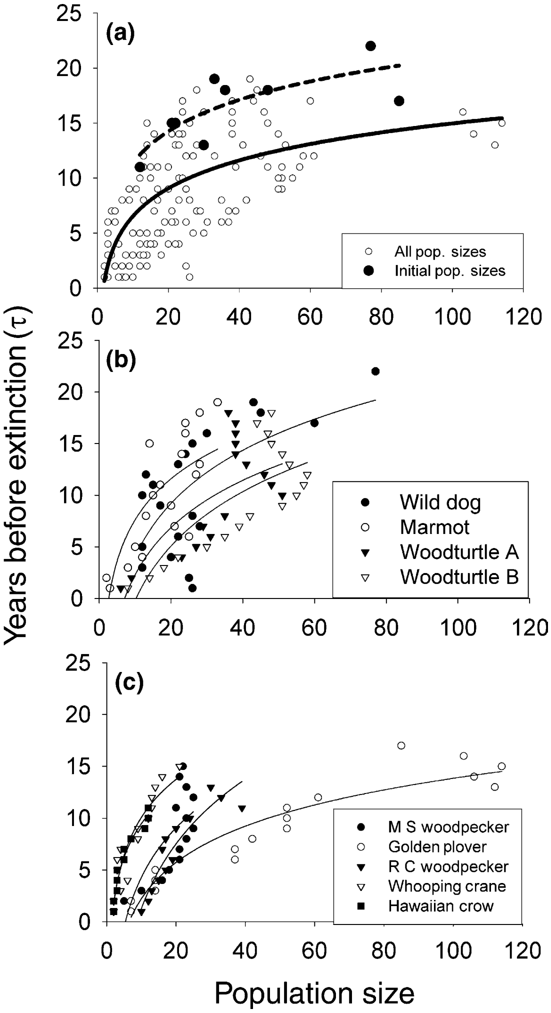

Figure 1 Time-to-extinction vs. population size vs. for nine wild populations of terrestrial vertebrates that were monitored to extinction. (a) Multilevel mixed regression with AR(1) autocorrelated error structure was used to fit a logarithmic curve to time series data aggregated across all nine populations (solid curve). This fit accounts for autocorrelation among censuses within time series and for unbalanced lengths across time series, but for simplicity we do not differentiate as to which census belongs to which population in the scatterplot. A separate logarithmic regression was fit to the collection of initial population sizes, one from each of the nine time series (filled circles; dotted curve). (b) Population lifetimes as a function of population size for two mammal and two turtle populations. (c) Population lifetimes as a function of population size for five bird populations. In (b) and (c), plotted curves are based on the empirical Bayesian estimates of the population-specific logarithmic slopes from the multilevel mixed regression across all nine populations.

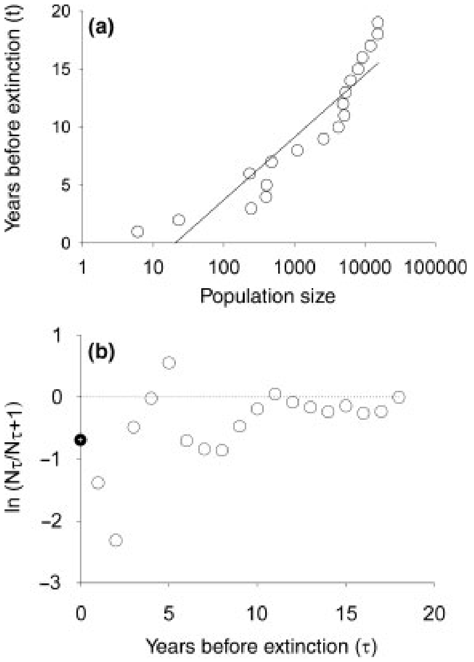

Figure 2 Extinction dynamics of coho salmon. (a) Population lifetimes as a function of population size (note log-scale on *x*-axis) and (b) rates of change in population size as a function of time-to-extinction. Filled symbol indicates the final decline resulting in extinction.

deteriorating even if one excluded the final transition to extinction. For the salmon, population declines also were larger closer to extinction ($P < 0.05$) (Fig. 2b).

Second, multilevel mixed regression on the squared residuals from the above analysis indicated that closer to extinction, in addition to the trend for steeper declines, population changes were also more variable. Specifically, the fitted multispecies regression model was $\text{Residual}^2 = 0.66 - 0.047 \times \tau$ ($P < 0.0001$). Population changes were still more variable closer to extinction even if we excluded large magnitude declines, such as the three largest year-to-year declines (all greater than eightfold) or the six largest year-to-year declines (all greater than fivefold). Population changes also remained more variable closer to extinction when we excluded the final year-to-year transition of each population, but the slope was not as steep: $\text{Residual}^2 = 0.22 - 0.012 \times \tau$ ($P < 0.001$). Our comparison model demonstrated a tendency for population changes to be more variable at smaller population sizes than at larger population sizes (the fitted multispecies regression model was $\text{Residual}^2 = 0.39 - 0.006 \times N_\tau$ ($P = 0.09$), but the time-dependent model afforded a slightly better fit (δ log-likelihood = 6.5, $P < 0.05$). For the salmon, population changes were significantly more variable closer to extinction ($P < 0.01$), but variability did not depend on population size. We note that the increased variability in

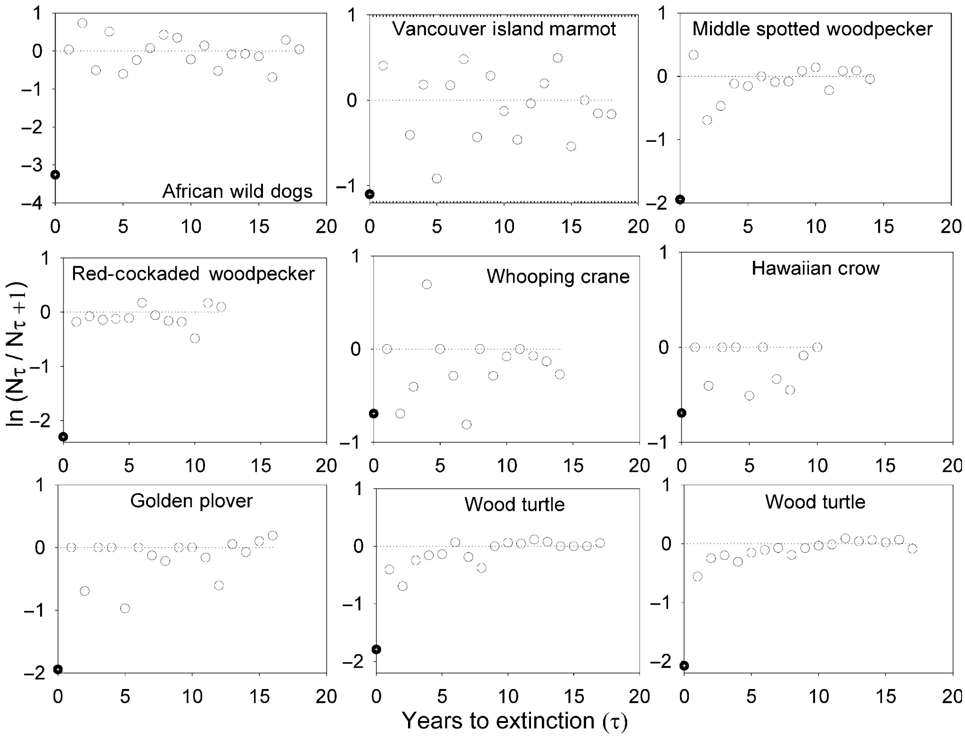

Figure 3 Changes in population size, plotted as year-to-year geometric growth rates against time-to-extinction, for nine populations of terrestrial vertebrates monitored as they declined to extinction. Filled symbols indicate the final declines resulting in extinction.

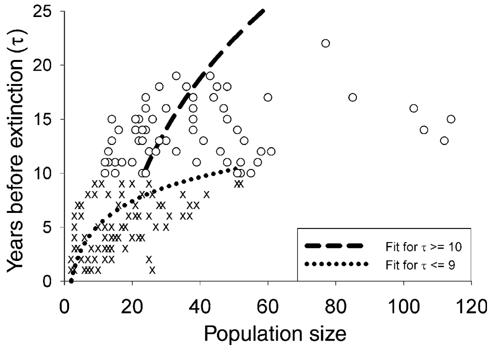

Figure 4 Population lifetimes as a function of population size for the aggregated data from nine terrestrial vertebrate populations (two mammals, two turtles, five birds). Multilevel mixed regression was used to fit logarithmic curves to all censuses 10 or more years prior to extinction [dashed curve fit to open circles; $y = -41.7 + 16.4 \times \ln(x)$], and to all censuses nine or fewer years prior to extinction [dotted curve fit to 'x' symbols; $y = -2.3 + 3.2 \times \ln(x)$]. These fits account for autocorrelation among censuses within time series and for unbalanced lengths across time series (which explains why the dashed curve visually appears to ignore the influence of the cluster of points on the right side of the graph, all of which come from a single time series).

year-to-year growth rates may be driven in large part by the final drop to extinction.

Third, adding time period ($\tau \leq 9$ vs. $\tau \geq 10$) as a categorical predictor variable to our multilevel mixed regression with AR(1) autocorrelated error structure, we found that over a range of population sizes (12–52 individuals), the logarithmic curve fit to censuses with $\tau \geq 10$ was significantly steeper than the logarithmic curve fit to censuses with $\tau \leq 9$ (Fig. 4; z-score for an effect of time period = 2.3, $P < 0.01$). This suggests that, after accounting for the differential contributions that particular populations made to the two time periods, a population size of n individuals ≤ 9 years before extinction was somehow 'less valuable' to persistence than the same population size several years further removed from extinction.

DISCUSSION

Attempts to characterize extinction risks across species and to develop management strategies for countering those risks necessitate a detailed understanding of the extinction process. Our work contributes to this understanding by quantitatively describing the trajectories by which several wild populations of vertebrates have gone extinct and testing two core predictions emerging from theoretical models of extinction risk. Though obviously regrettable from the perspective of local conservation efforts, these actual extinction events provide important lessons about the nature of extinction dynamics for wild vertebrates – lessons that have otherwise only been examined with theoretical models (e.g. Lande *et al.* 2003), laboratory experiments (e.g. Belovsky *et al.* 1999), or island invertebrates (e.g. Schoener *et al.* 2003).

Our analyses confirmed two long-standing theoretical predictions concerning the dynamics of extinction-bound populations. First, in accordance with theoretical models of population dynamics, we found for populations that go extinct, time-to-extinction scales logarithmically with population size (Figs 1 and 2a). We mention in passing that, if considered individually, the five bird populations generally conform more closely to the predicted logarithmic scaling relationship than do either the mammals or the turtles. The source of this pattern is unclear, although it seems plausible that among-population differences in the importance of species interactions to observed declines might be an important contributing factor. Disease and harvesting by humans are hypothesized to be important for the wild dog and turtle populations, respectively (Garber & Burger 1995; Ginsberg *et al.* 1995). When a larger database of time series becomes available, an interesting next step would be to develop scaling factors (perhaps based on species' life history characteristics, trophic level, and similar ecological traits; Fagan *et al.* 2001; Pereira *et al.* 2004) that could help explain the interspecific variation in the dependence of population lifetime on population size (Table 1).

Regarding the second prediction, three lines of evidence suggest that these extinction-bound populations collectively exhibit dynamics akin to those theoretically proposed to occur in extinction vortices (Gilpin & Soulé 1986). First, across populations, year-to-year rates of decline were larger for smaller values of time-to-extinction, implying that aspects of the populations' dynamics did in fact deteriorate as extinction neared (Figs 2b and 3). We also found that year-to-year declines in population size were larger for smaller population sizes, but time-to-extinction proved a stronger predictor variable across species.

Second, we found that, across populations, detrended variability in year-to-year rates of decline increased as extinction neared. In general, we fully expect that population size should make important contributions to such variability via demographic stochasticity (Gilpin & Soulé 1986; Lande 1993; Lande *et al.* 2003), but our data set revealed at best a marginally significant effect of population size on detrended variability, presumably because of the imperfect correlation between time-to-extinction and population size.

Third, the difference between the logarithmic curve fits to aggregated data for censuses greater than or less than 10 years prior to extinction (Fig. 4) suggests that a population size of n individuals a few years before extinction was somehow less valuable to persistence than the same population size several years earlier. This pattern accords with predictions about the importance of inbreeding, effective population size, and related demographic problems in declining populations as extinction nears (Gilpin & Soulé 1986; Lande *et al.* 2003). However, lacking genetic data or estimates of effective population size, we cannot test directly whether such mechanisms were operating in these populations.

Our regression results in which both the magnitude of population changes and detrended variability in population changes depended significantly on time-to-extinction imply that estimation of extinction parameters from rates of decline and levels of variability observed a decade or more before extinction are likely to underestimate the actual probability of extinction. This finding contrasts with our previous results (Holmes & Fagan 2002; Holmes 2004, E.E. Holmes and W.F. Fagan, unpublished data), which found that probabilities of declines to critical quasi-extinction thresholds other than actual extinction ($n = 1$ or 0) were well-characterized by diffusion models using parameter estimates obtained a decade or two before quasi-extinction. This emphasizes the importance of characterizing critical population thresholds ($> n = 0$ or 1) for at risk populations. Declines to quasi-extinction thresholds appear much more predictable than do declines to actual extinction. The latter appear to be characterized by a vortex of increasing variability and increasing rates of decline.

A small data set like the one, we considered here suffers from a variety of potential biases and affords limited opportunities for quantitative analyses. Nevertheless, based on the overall consistency of our findings, we conclude that, collectively, the extinction dynamics of these wild vertebrate populations do accord with core theoretical predictions about the process of extinction. Part of the difficulty in finding examples of well-monitored declines to extinction is that so many extinction events (whether natural or human-aided) go unnoticed. Sporadic monitoring efforts, such as those devised to characterize the conservation status of little-known species (Hilton-Taylor 2000; World Conservation Union 2001), do not provide the same level of detail about extinction dynamics as do regular efforts to enumerate wild populations, so it is important to make full use of those few cases where we have more detailed coverage of dynamics. Ironically, long-term monitoring programmes also contribute to the lack of detailed knowledge about how populations go extinct. This is because when a monitoring programme reveals a population to be declining consistently, managers may be forced to take direct action to stem the decline or save the species. The California condor is a good example. The last wild population of that species was observed to decline from over 50 birds to 12 over just 11 years, at which point managers decided to capture the surviving individuals for safekeeping and breeding at a captive rearing facility (Snyder & Snyder 2000). Decisions about when to initiate captive breeding or *in situ* intensive management efforts (such as supplemental feeding) constitute one context in which knowledge gained from well-monitored extinction events might be especially useful to managers. In particular, information about the trajectories by which populations approach extinction (Fig. 1) and thresholds below which no increases in population size are likely to occur (Table 1) could prove useful in developing intervention guidelines, such as when to withdraw the last remaining individuals of a species from the wild. The limited data at hand suggest a quite conservative strategy may be warranted because of the potential for sudden extinction events, even in well-monitored populations.

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