Risk-Based Viable Population Monitoring

DAVID F. STAPLES,*‡ MARK L. TAPER,* AND BRADLEY B. SHEPARD*†

*Montana State University, Department of Ecology, 310 Lewis Hall, Bozeman, MT 59717-3460, U.S.A.
†Montana Fish, Wildlife, and Parks, Region 3, 1400 South 19th Avenue, Bozeman, MT 59718-5417, U.S.A.

Abstract: *We describe risk-based viable population monitoring, in which the monitoring indicator is a yearly prediction of the probability that, within a given timeframe, the population abundance will decline below a prespecified level. Common abundance-based monitoring strategies usually have low power to detect declines in threatened and endangered species and are largely reactive to declines. Comparisons of the population's estimated risk of decline over time will help determine status in a more defensible manner than current monitoring methods. Monitoring risk is a more proactive approach; critical changes in the population's status are more likely to be demonstrated before a devastating decline than with abundance-based monitoring methods. In this framework, recovery is defined not as a single evaluation of long-term viability but as maintaining low risk of decline for the next several generations. Effects of errors in risk prediction techniques are mitigated through shorter prediction intervals, setting threshold abundances near current abundance, and explicitly incorporating uncertainty in risk estimates. Viable population monitoring also intrinsically adjusts monitoring effort relative to the population's true status and exhibits considerable robustness to model misspecification. We present simulations showing that risk predictions made with a simple exponential growth model can be effective monitoring indicators for population dynamics ranging from random walk to density dependence with stable, decreasing, or increasing equilibrium. In analyses of time-series data for five species, risk-based monitoring warned of future declines and demonstrated secure status more effectively than statistical tests for trend.*

Key Words: population modeling, population viability analysis, PVA, species recovery, threatened and endangered species

Monitoreo de Poblaciones Viables con Base en Riesgos

Resumen: *Describimos el monitoreo de poblaciones viables basado en riesgos, en el que el indicador del monitoreo es la probabilidad de que la abundancia de la población decline, en un período de tiempo determinado, por debajo de un nivel predefinido. Las estrategias comunes de monitoreo basadas en la abundancia generalmente tienen poco poder para detectar declinaciones de especies amenazadas y en peligro y son ampliamente reactivas a las declinaciones. Las comparaciones del riesgo de declinación estimado a lo largo del tiempo ayudarán a determinar el estatus de una manera más defendible que con los métodos de monitoreo actuales. El monitoreo de riesgo es un método más preventivo; es más probable que los cambios críticos en el estatus de una población sean evidentes antes de una declinación devastadora que con métodos de monitoreo basados en la abundancia. En este marco, la recuperación está definida como el mantenimiento de un bajo riesgo de declinación para varias generaciones futuras y no solo como una evaluación de la viabilidad a largo plazo. Los efectos de los errores de las técnicas de predicción de riesgos son mitigados mediante intervalos de predicción más cortos, el ajuste de umbrales de abundancia cerca de la abundancia actual y la incorporación explícita de la incertidumbre en las estimaciones de riesgo. Intrínsecamente, el monitoreo de poblaciones viables también ajusta el esfuerzo de monitoreo en relación con el verdadero estatus de la población y muestra considerable robustez ante errores de descripción del modelo. Presentamos simulaciones que muestran que las predicciones de riesgo derivadas de un modelo simple de crecimiento exponencial pueden ser indicadores efectivos del monitoreo de la dinámica poblacional que varían de caminatas al azar hasta denso dependencia*

1908

con equilibrio estable, decreciente o creciente. En el análisis de datos de series de tiempo para cinco especies, el monitoreo basado en riesgo alertó sobre futuras declinaciones y demostró el estatus seguro más efectivamente que las pruebas estadísticas de la tendencia.

Palabras Clave: análisis de viabilidad poblacional, AVP, especies amenazadas y en peligro, modelado de poblaciones, recuperación de especies

Introduction

Correctly evaluating the status of threatened and endangered populations is critical to detecting population declines that will further endanger the population and to verifying effectiveness of conservation actions. Monitoring to detect changes in status is frequently specified in recovery plans (Morris et al. 2002). Unfortunately, detecting changes in status with commonly used monitoring strategies such as monitoring species abundance and statistical tests (Thompson et al. 1998) for population trend can be difficult (Holmes & York 2003). Because of high variability in ecological data arising both from natural variation in population growth and from measurement errors in population estimates, a biologically devastating decline could occur before there is a reasonable chance to detect the decline. For example, at observed variation levels common in bull trout (*Salvelinus confluentus*) data, a population could decline by more than 60% before the power to significantly detect such a decline reached 0.80 (Maxell 1999). For species that have presumably already declined to low levels, an inability to quickly detect further declines in population abundance is a serious problem. Ideally, monitoring would reliably detect a small (though biologically relevant) decline in a short amount of time; this goal, however, is not realistic with current methods for most populations. Monitoring species with abundance-based methods also leaves managers in a reactive posture because a decline might be demonstrated only after it has seriously diminished the population, even though the demographic problems that caused the decline occurred many years before the decline was "significant."

Natural variation inherent in population data also complicates the task of determining whether a population is recovering following actions designed to promote recovery. Conservation actions are usually costly and may be controversial, but many years of monitoring will often be required before the effects of these actions can be evaluated clearly through population abundance estimates. Compounding these problems is a common lack of biologically based recovery criteria in population monitoring plans. Consequently, populations are rarely delisted (unless they go extinct) because there is no agreed upon method for evaluating population status and levels for recovery are rarely specified. Even when a species has re-bounded and might be considered recovered, the lack of quantifiable recovery criteria applied to a statistically rigorous monitoring protocol prevents agencies from concluding the population is secure.

There have been recent calls to incorporate population viability analysis (PVA) in endangered species recovery plans (Morris et al. 2002; Lande et al. 2003). With PVA methods, it is possible to predict future population abundance, the time to extinction (or some other lower threshold abundance), the probability of reaching a lower threshold, or of the probability of reaching a lower threshold within a specified amount of time (Dennis et al. 1991; Morris & Doak 2002). Morris et al. (2002) give three useful functions of PVA in recovery planning. First, PVA methods can help identify particular life stages or demographic processes that should be targeted to promote recovery (Caswell 2000, 2001). Model analyses can both focus management actions and help guide planning of data collection to improve predictive accuracy. Second, PVA can serve as a means to synthesize data for assessing recovery success. For example, monitoring data on population abundance and environmental correlates can be combined with demographic models for PVA projections to give a more comprehensive picture of population status (Morris et al. 2002; Lande et al. 2003). Finally, PVA can provide good estimates of relative risks to populations with as little as 10 years of data (McCarthy et al. 2003). Measures of risk can be successfully compared among populations to provide a relative measure of how urgently recovery actions need to be implemented in specific populations, or risk can be compared for the same population under competing conservation strategies (Ellner et al. 2002).

This documented accuracy of relative risk assessments suggests that an individual population could also be compared to itself over time for an indication of how the population's risk of decline is changing over time. Monitoring risk in this fashion is also more concordant with the definitions of endangered ("in danger of extinction") and threatened ("likely to become endangered in foreseeable future") in the U.S. Endangered Species Act (ESA) of 1973 (as in U.S. Code 2000). There is also the opportunity to develop biologically relevant and adaptable recovery criteria for threatened and endangered species with a risk-based monitoring plan. As an alternative to abundance-based monitoring methods, we propose a

risk-based viable population monitoring (VPM) protocol in which yearly risk predictions are used as the monitoring indicator.

Threatened and endangered populations are likely to be at low abundance levels; consequently, two important management goals are to prevent further declines to unsustainable levels and to facilitate increases to a secure abundance level. Given these objectives, an estimate of the risk of the population declining below a biologically relevant threshold is a useful monitoring indicator that consolidates relevant information about the population's status. For monitoring purposes, risk is defined as the probability of population abundance declining below a lower threshold within a given time frame. Increases in this risk over time indicate that the population's status is deteriorating and remedial actions should be implemented. Conversely, decreases in risk demonstrate that management actions are reducing the likelihood of a catastrophic decline in the near future. A population could be considered secure after a period (e.g., 10 years) of consistently low risk; in the VPM framework, however, recovery is not a one-time evaluation but the maintenance of low risk of a serious population decline. By comparing predicted risk over time, VPM can provide more defensible status evaluations and help facilitate better communication between agencies as to what constitutes a healthy or threatened population.

Methods

A common situation in monitoring is when the target population is undergoing so-called random-walk population growth. In this case, the long-term population growth rate is zero but observed growth could be positive or negative in any given year because of environmental variation. At any time, a series of bad years (or even one *really* bad year) could cause a large drop in abundance. Random-walk population growth will, by definition, tend to give trend estimates that are not different from zero. This makes monitoring based on trends in abundance alone unreliable. If the population has a significant negative or positive growth rate, it will more likely be apparent with a few years of data. To evaluate how a VPM strategy will perform for such a population, we simulated a random-walk process for 15 years with an initial abundance of 1000. We then estimated the risk of the population abundance declining below 500 within 5 years (denoted PLT5) or within 10 years (PLT10) with an exponential growth population model (Dennis et al. 1991; Morris & Doak 2002). The random-walk simulation continued for 50 additional time steps, with updated estimates of PLT5 and PLT10 calculated at each time step with the entire data series up to that point (i.e., risk estimated with 15, 16, and 17 years of data, and so on until the end of the series). We compared the population's abundance trajectory with the series of estimated risk metrics.

The risk calculations in VPM should be based on the best available model of the target population's dynamics. In reality, the true population dynamics are unknown and it can be difficult to discern between competing models (e.g., density independent or dependent growth) in most data series (Zeng et al. 1998). For this reason, it is instructive to evaluate VPM when the incorrect model is used for analysis (i.e., when the actual population growth is density dependent but risk is estimated with an exponential growth model). We used three density-dependent models to generate time series that were analyzed with VPM using an exponential growth PVA. The first model was a population with a stable equilibrium slightly above the lower threshold, a very different process but potentially indiscernible from random-walk population growth in actual data. The second was a population with a slowly declining (1% per year) carrying capacity, such as could result from gradual degradation of habitat over time. The third scenario was an increasing (3% per year) carrying capacity, which should test whether VPM can detect when a population is on the path to recovery. We compared the estimated risk from an exponential growth analysis with the true risk calculated with simulations of the density-dependent model.

To see whether a risk-based monitoring strategy can warn of potential declines and demonstrate population security more reliably than testing for a significant trend in abundance, we also applied VPM in a post hoc evaluation of four historical time series of population data: 1965–1980 surveys of California Condor (*Gymnogyps californianus*; Snyder & Johnson 1985), 1969–1989 censuses of Puerto Rican Parrot (*Amazona vittata*; Dennis et al. 1991), 1938–1993 winter counts of Whooping Crane (*Grus americana*; USFWS 1994), and 1959–1997 adult female estimates for grizzly bear (*Ursus arctos horribilis*; Morris & Doak 2002). To prevent bias and low power resulting from sampling errors in the data, parameters for risk estimates and tests for trend were calculated using the exponential growth PVA method presented in Staples et al. (2004). Exponential growth PVA analyses and trend estimation for these data sets have been discussed previously (Dennis et al. 1991; Staples et al. 2004). For the analysis of these data sets, the lower threshold was arbitrarily set at one-half the initial population estimates. Because the grizzly data are running 3-year sums, the prediction interval for that data series was set at 20 years; for all others it was set at 5 years. All significance tests for trend were two-sided with test size at 0.10. We calculated risk estimates and tests for significant trend yearly starting after the first 5 years of observations.

We also analyzed a contemporary data set of index counts of spawning nests, or redds, for bull trout (*S. confluentus*) from the Flathead River drainage in northwestern Montana (U.S.A.). Although redd count data have been collected on this population consistently since 1980, major community changes in Flathead Lake around 1990 caused an explosion in lake trout (*S. namaycush*)

abundance that altered the dynamics of this bull trout population. These changes most likely precipitated a large crash in the bull trout population observed between 1991 and 1992 (Deleray et al. 1999). Because PVA predictions with an exponential growth model assume a constant process (i.e., the true nature of population growth remains the same) and no catastrophic environmental events, only data collected since the system stabilized (approximately 1992) were deemed appropriate for the VPM analysis.

The bull trout data are not direct counts of individuals but of spawning sites; therefore it would be useful to define the analysis in terms of a biologically significant adult abundance. In this case we set the lower threshold for adult abundance at 1000 spawning adults based on the estimated effective population size necessary to maintain genetic diversity in the populations (Rieman & Allendorf 2001). Assuming 3.2 fish/redd (Fraley & Shepard 1989) and the total redd to index redd count relationship observed by Deleray et al. (1999) yields a calculated lower threshold of 125 for the index redd counts. (Much of the data for these conversions were collected before the population crash and it is unknown whether these conversions hold for the current population.) As in the above data analysis, the estimated probability of redd counts declining below the lower threshold within 5 years was calculated yearly starting with 5 years of observations. Changes in probability of redd counts declining below 125 should then reflect the changes in the risk of declining below 1000 spawning adults, subject to the accuracy of the conversions.

Results

In random-walk simulations, VPM risk estimates effectively warned of future declines in population abundance; because risk estimates are a probability of future decline,

however, a high risk estimate does not necessitate a future decline. In an example of simulated random-walk growth, the initial risk estimates were high because of negative trend and high variance estimates (Fig. 1). After a period of steady increases in abundance, the risk estimate dropped; after 2 years of decline, however, there was a sharp increase in estimated risk. This increase was due to lower abundance and a downturn in the estimated trend. As time passed, the estimated risk declined because of higher abundance and more stable estimates of both trend and process variation. The only trend estimate that was close to being significantly < 0 was the first estimate, which was calculated with only five observations ($p = 0.08$; one-sided test). Trend estimates converged on the true value of 0, as expected, indicating tests for a significant trend would not be very informative for monitoring a population with random-walk dynamics. Although risk estimates calculated with the 10-year prediction interval were higher, trends in risk estimates from the 5- and 10-year prediction intervals were similar.

For density-dependent simulations with stable equilibrium abundance, VPM analysis with the exponential growth model showed biased high-risk estimates for abundance levels below equilibrium and biased low-risk estimates for abundances above equilibrium (Fig. 2). These biases were due to the discrepancy between the exponential growth analysis model and the true density-dependent process. An exponential growth model does not account for increases in the growth rate as the population gets further below equilibrium or overcompensatory effects that can lead to severe crashes directly from abundances above equilibrium. High true risk at abundances above equilibrium is an idiosyncrasy of the Ricker model used for the simulations (Ripa & Lundberg 2000). Other types of density-dependent population growth do not necessarily have high risk of decline directly from high abundances.
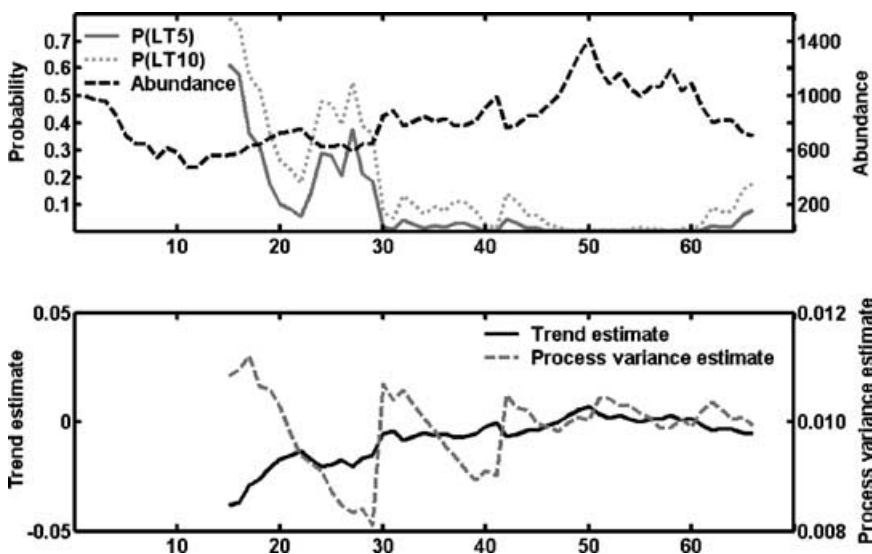

Figure 1. (top) Simulated random-walk population growth with predicted probabilities for declining below a threshold value within 5 years (PLT5) and 10 years (PLT10) calculated with an exponential growth model. (bottom) Trend and process variance estimates used to calculate PLT5 and PLT10.
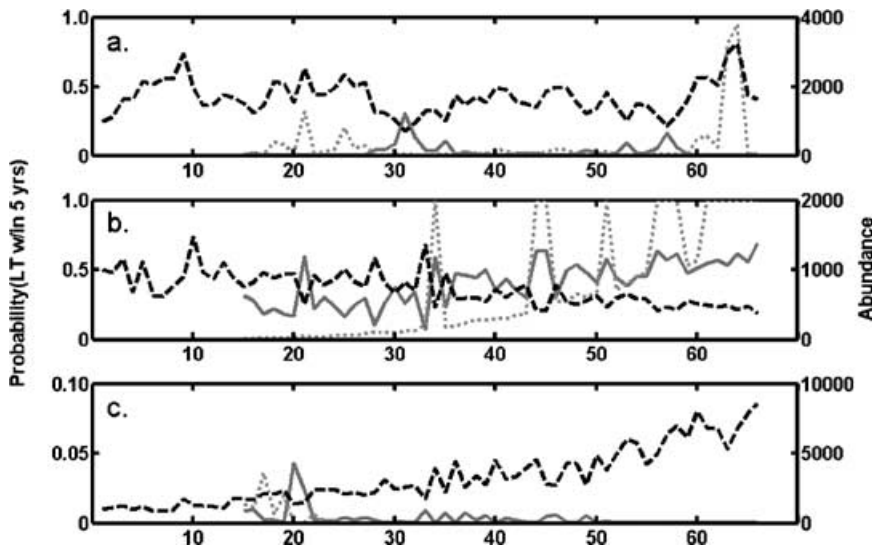
Figure 2. Estimated probability of a population declining below 500 within 5 years calculated with an exponential growth model from simulations of density-dependent population growth with equilibrium value (a) stable, (b) declining 1% per year, and (c) increasing 3% per year; dashed line, population abundance; dotted line, true probability of declining below lower threshold (LT); solid line, estimated probability of declining below 500 within 5 years.

When the equilibrium abundance was declining over time, risk estimates generally increased over time, corresponding to decreases in abundance. These risk estimates were stochastic but never < 0.10 for consecutive estimates. In contrast, with classical trend analysis, there were no significant tests for negative trend for the entire series (lowest p value = 0.32; one-sided test). In situations when the equilibrium was increasing over time, VPM generally showed low risk, with estimated risk usually < 0.01. Risk increased to 0.05 once when the abundance declined at time 20. Again, no classical tests showed a trend of > 0 despite the long data series (lowest p value = 0.21; one-sided test). In contrast to the results with classical methods, this population could be considered secure according to VPM when, for example, the risk of decline was < 0.01 for 5 consecutive years. True recovery should also be viewed as maintaining low risk of decline, however, not just a one-time evaluation of status.

In analyses of historical data sets, VPM warned of future declines and demonstrated secure status before such changes in abundance could show even a marginally significant trend (Fig. 3). Increased risk occurred after only 6 years of observations for the sharply declining California Condor population, and after 9 years of observations, the estimated probability of declining below the threshold was 0.80. In contrast, the only significant trend estimate made in the Condor series occurred after 13 years of observations ($p < 0.10$; two-sided test). For populations that were increasing, as was the case for the Puerto Rican Parrot and Whooping Crane, the VPM analysis demonstrated low risk before any significant trends in abundance were detected. For the Puerto Rican Parrot, there was a general decline in estimated risk from an initially high estimate. Predicted risk was quite low after 10 years of observations and near 0 after 14 years; there was, however, no significant trend estimate for the entire data series. In the
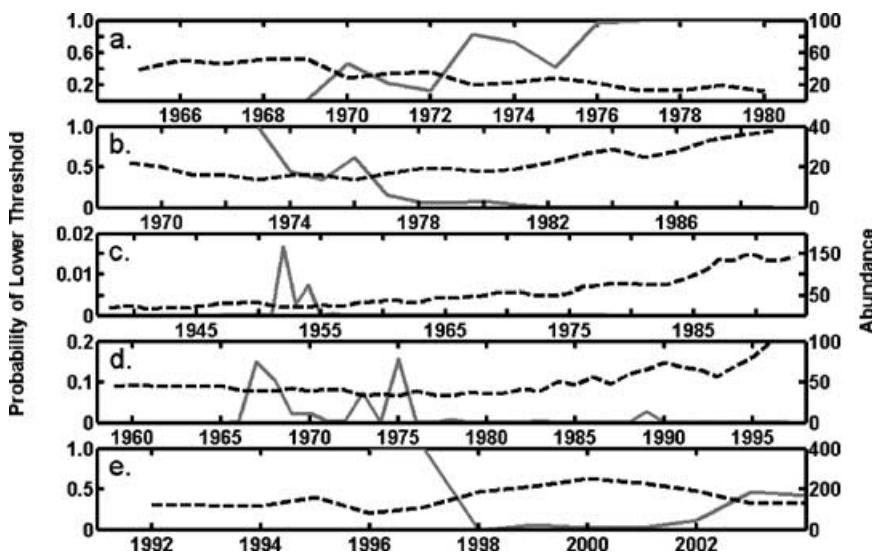

Figure 3. Viable population monitoring analysis for (a) California Condor, (b) Puerto Rican Parrot, (c) Whooping Crane, (d) grizzly bear, and (e) bull trout; dashed line, estimated population abundance except for bull trout (e), in which case it is index redd counts; solid line, probability of the population declining below lower threshold within 5 years (a,b,c,e) or 20 years (d). Threshold is one-half the initial population estimates for a, b, c, and d; threshold is 125 redds for (e).

case of the Whooping Crane, the risk estimates initially were 0 and only increased above 0.01 for 1 year. There was no significant trend in Whooping Crane abundance until there were 41 years of observations. The grizzly bear analyses showed significantly negative trend estimates for 1973–1980. This period was preceded by higher and more volatile risk estimates for 1967–1975. Grizzly bear abundance increased after 1980 and subsequent risk estimates were low; there were, however, no significant trend estimates after 1980.

Between 1992 and 1996, counts of bull trout redds declined below the threshold; therefore the initial estimated risk of going below 125 redds was 1 (Fig. 3). Redd counts for the next 4 years, however, sharply increased and, by 2000, they were double the 1992 level. Consequently the estimated probability of decline below the threshold decreased to nearly 0. Unfortunately, redd counts have steadily declined since 2000, which has resulted in increasing risk estimates. The steep increase in estimated risk is evidence that the likelihood of declining below 1000 total spawners increased since 2001 despite the uncertainty about the true risk at the present. It is too early to come to any long-term conclusions about the population because of relatively few years of observations and the coarse prediction method used for this analysis (i.e., an exponential growth model was used to predict adult numbers in an age-structured population with a long pre-reproductive period).

Discussion

Because VPM focuses on monitoring risk, it offers several improvements over traditional strategies. Management of threatened and endangered populations can be more proactive in addressing problems. Increases in risk should be evident and remedial actions could be initiated before large declines in abundance. For example, VPM showed large increases in risk for the California Condor data series well before any precise estimates of trend would have been available. In a similar manner, VPM can demonstrate improvements in population status before traditional methods. For the Puerto Rican Parrot analyses, risk estimates were 0 for the last 9 years but there were no significant trend estimates for the entire series.

A risk-based monitoring strategy has an intrinsic mechanism to adjust monitoring effort in relation to the population's true status. More precise predictive ability lowers the calculated risk. Conversely, uncertainty in predicted abundance results in higher estimated risk. A stable population well above the lower bound may have high estimated risk entirely because little is known about it (i.e., predictions about future abundance are very wide). As more is learned, population abundance predictions will be more precise, thereby reducing the estimated risk

without the population's true status changing. Populations near the lower bound are likely to require more precise abundance predictions to demonstrate secure status. In contrast, minimal monitoring effort will be required for populations far above the lower bound because less precise predictions will still lead to low risk estimates.

Abundance thresholds are used to lessen prediction errors and can lead to more robust monitoring in face of possible catastrophic declines. Thresholds set near observed abundance levels help prevent errors that would arise from large increases in demographic stochasticity (Lande 1993) or changes in population dynamics such as the Allee effect (Dennis 1989; Courchamp et al. 1999) that may occur at abundances near extinction. The abundance threshold may also be modified to incorporate the effects of catastrophes. It would be reasonable to raise the threshold to the level where the population would still be viable after a likely catastrophe (see Ralls et al. 1996 for an example).

Shorter prediction intervals decrease prediction errors that are problematic in PVA techniques (Ludwig 1999) and results in biased risk estimates. Although long-term (e.g., 100-year) predictions may not be meaningful, it might be possible to reliably estimate short-term risk (Fieberg & Ellner 2000). The ideal prediction interval most likely will depend on the monitored population. Our analyses of the Whooping Crane data suggested that a 5-year prediction interval was not very sensitive for monitoring purposes. A prediction interval of 10 years or more is probably warranted for longer-lived species such as the Whooping Crane. An even better strategy may be to monitor several prediction intervals concurrently, with interval selection based on the generation length of the target species. One possibility is to monitor the probability of declining below the threshold abundance within one, two, and five generations. Additionally, the nature of the data itself may necessitate a longer prediction interval. The grizzly bear data are 3-year sums of adult females with cubs, so it is unlikely that a 5-year prediction interval will be very sensitive to population changes, especially considering the long lifespan and generation time of the grizzly bear.

For many populations, data are inadequate to discern between competing population models (e.g., differentiate between density-independent and -dependent growth). Comparison of risk estimates from an exponential growth model may provide a practical method for assessing the changes in risk for a variety of populations. In our simulations, predictions made with a simple exponential growth model appeared to be useful for monitoring populations with a range of underlying growth processes. A density-independent approximation correctly or conservatively estimates the risk of severe decline for a broad range of density-dependent processes and is most accurate when it matters most to conservation managers (i.e., when a population is fluctuating near its carrying

capacity, recovering slowly, or declining toward extinction) (Sabo et al. 2004). Additionally, any effect of biases in risk estimates on the inference to population status is reduced because VPM relies not on a single risk estimate but on comparison of risk estimates over time.

The usefulness of this approximation depends on how well exponential growth can characterize actual population growth patterns. When the equilibrium for a density-dependent population is increasing, for example, resulting abundance trajectories will have similar behavior as an exponential growth process (i.e., observed population abundance is variable around an increasing mean abundance). In our simulations, the estimated trend from the exponential growth model converged on the true rate of change for both increasing and decreasing carrying capacities. Similarly, stable density-dependent growth can behave like a random walk if observed population abundance varies around the same mean abundance. In such cases the exponential growth approximation of the distribution of population abundance can be useful, especially for shorter prediction intervals. Again, the approximation will overestimate risk for abundances below equilibrium. It may be reasonable, however, to view a density-dependent population close to a critical lower threshold as at higher risk because declining abundance could be a signal of deteriorating habitat reducing the equilibrium abundance. For strong overcompensatory density-dependent growth, however, where overshoot is possible, an exponential growth analysis will underestimate risk for a population above equilibrium.

Certainly in some monitoring situations, an exponential growth analysis, as presented above, will be of little practical use. This may be simply due to the lack of a suitable data time series with which to estimate the risk. If there are no such data, it is likely to take up to a decade or more before there are enough data for reasonably precise abundance predictions (Morris & Doak 2002). Even when there are suitable data, the exponential growth approximation of the true biological process may be too inaccurate for useful predictions, especially if current abundance is close to the threshold. In such cases it is possible to construct more detailed demographic models for more precise predictions in a VPM analysis. Models that are more detailed may produce relatively reliable monitoring indicators more quickly than waiting for enough yearly observations so that the exponential growth analysis can be reasonably applied. Estimating demographic parameters for such models, however, may be expensive. The bull trout population analyzed above is an example of the latter situation in that current redd counts are close to the threshold and the exponential growth approximations are imprecise because of fluctuations in age-class abundances.

Bull trout have been monitored for more than 20 years in the Flathead with index redd counts, and although the above analysis demonstrates an uncertain future for the population, the process by which redd counts change over time is not well approximated by an exponential growth process (i.e., this year's redds are not a direct function of last year's redds). There is the possibility for age-class interactions to generate cycles in adult abundances that confound the use of an exponential growth model. This population has a maturation time of approximately 6 years and the potential for density-dependent interactions among juvenile cohorts that can cause large fluctuations in age-class abundances (Paul et al. 2000). We have found that risk predictions from an exponential growth model based on adult-only data are biased high if the population experiences severe age class fluctuations (D.F.S. & M.L.T., unpublished data). Holmes (2001) simulated adult salmon abundances with an age-based model and also found that using adult abundance counts as a surrogate for total population size led to severe bias in estimators of trend and process variation, even with no sampling error. It is likely that structural differences between the true biological process and predictive model results in overestimates of risk in the VPM analysis above. This implies abundance levels would have to be very high relative to the threshold for this redd-based risk analysis with the exponential growth model to show low risk. We are working to improve prediction models for this population, and remedial actions are being implemented to increase bull trout population abundance.

To decrease controversy about population status and facilitate communication among management agencies, establishing a priori goals for recovery is a critical feature of a monitoring strategy. Schultz and Hammond (2003) recommended a recovery goal for Fender's blue butterfly (*Icarica icarioides fenderi*) based on the minimum population growth rate necessary for 100-year persistence. In this case, high variation in population growth and a long prediction interval led to the conclusion that a relatively high population growth rate would be necessary for persistence (minimum average growth rate of $\lambda = 1.55$ over 10 years). This goal may be difficult to achieve in practice, especially if there are density-dependent interactions within the population. Alternatively, it may be constructive to view recovery not as a one-time verification of long-term persistence, but as maintaining low risk of a biologically relevant decline within the next few generations. Very long prediction intervals compound uncertainty and require the assumption that environmental conditions and the growth process itself remain the same far into the future, making it very difficult to verify long-term viability satisfactorily.

Recovery criteria based on maintaining low risk can be a more tangible and achievable goal for managers of threatened and endangered species. Several broad categories of recovery criteria have been used for threatened and endangered species: population size, population trend, habitat fragmentation, demographic rates, and legal or policy criteria (Gerber & Hatch 2002). There is

also concern that monitoring tasks specified in recovery plans do not adequately address specific threats affecting populations (Campbell et al. 2002) or that recovery criteria are poorly linked to species biology (Schultz & Hammond 2003). A risk-based strategy can consolidate these broad categories of recovery criteria into a single, biologically relevant criterion with flexibility to assess specific threats relative to their effect on the population's risk of decline. An added advantage is that risk-based recovery criteria can adapt to unanticipated threats to a population after delisting.

A useful characteristic in VPM is that the measure of status is congruent with the definitions of *threatened* and *endangered* under ESA and could lead to less controversy about delisting species. The primary difficulty in delisting is that there is no regulatory mechanism to address threats to a population except for the ESA. A population is delisted only if there are protections for the population from all known threats under other existing laws (Doremus & Pagel 2001). It may be possible to develop a regulatory mechanism that provides a means to address and adapt to threats after delisting with risk-based recovery criteria. In VPM, recovery is defined as perpetually maintaining low risk of decline for the population or, in other words, a low probability that the population would qualify as threatened or endangered. After delisting, management agencies could manage a population as it sees fit as long as the requirement of low risk of decline is satisfied.

Unlike conventional monitoring methods, VPM answers a fundamentally different question. The goal of VPM is to estimate how the population's status is changing (i.e., toward recovery or extinction) given current conditions instead of proving a past decline was significant. The significance value for classical tests for trend is strictly on what has happened in the past. Conversely, VPM uses prediction intervals about future abundance for inference on population status. Risk-based monitoring should show increases in risk for declining populations to signal the need to implement conservation actions. To establish recovery, low risk of decline to untenable levels must be demonstrated and maintained. Further work is needed to determine exactly what constitutes a critical increase in risk or a stable, secure population through viable population monitoring. Risk-based monitoring can be a valuable tool for managing threatened and endangered species because it is proactive in detecting potential population declines and can show how a population's status is changing relative to consistent, biologically relevant recovery criteria.

Acknowledgments

Literature Cited

Campbell, S. P., J. A. Clark, L. H. Crampton, A. D. Guerry, L. T. Hatch, P. R. Hosseini, J. J. Lawler, and R. J. O'Connor. 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecological Applications **12:**674–681.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology **81:**619–627.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology & Evolution **14:**405–410.

Deleray, M., L. Knotek, S. Rumsey, and T. Weaver. 1999. Flathead Lake and River system fisheries status report. Montana Fish, Wildlife, and Parks, Kalispell.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling **3:**481–538.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs **61:**115–143.

Doremus, H., and J. E. Pagel. 2001. Why listing may be forever: perspectives on delisting under the U.S. Endangered Species Act. Conservation Biology **15:**1258–1268.

Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. Conservation Biology **16:**258–261.

Fieberg, J., and S. P. Ellner. 2000. When is it meaningful to estimate an extinction probability? Ecology **81:**2040–2047.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lale and River system, Montana. Northwest Science **63:**133–143.

Gerber, L. R., and L. T. Hatch. 2002. Are we recovering? An evaluation of recovery criteria under the U.S. Endangered Species Act. Ecological Applications **12:**668–673.

Holmes, E. E. 2001. Estimating risks in declining populations with poor data. Proceedings of the National Academy of Sciences of the United States of America **98:**5072–5077.

Holmes, E. E., and A. E. York. 2003. Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. Conservation Biology **17:**1794–1806.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist **142:**911–927.

Lande, R., S. Engen, and B.-E. Saether. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, New York.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology **80:**298–310.

Maxell, B. A. 1999. A power analysis on the monitoring of bull trout stocks using redd counts. North American Journal of Fisheries Management **19:**860–866.

McCarthy, M. A., S. J. Andelman, and H. P. Possingham. 2003. Reliability of relative predictions in population viability analysis. Conservation Biology **17:**982–989.

Morris, W. F., P. L. Bloch, B. R. Hudgens, L. C. Moyle, and J. R. Stinchcombe. 2002. Population viability analysis in endangered species

recovery plans: past use and future improvements. Ecological Applications **12:**708–712.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.

Paul, A. J., J. R. Post, G. L. Sterling, and C. Hunt. 2000. Density-dependent intercohort interactions and recruitment dynamics: models and a bull trout (*Salvelinus confluentus*) time series. Canadian Journal of Fisheries and Aquatic Sciences **57:**220–1231.

Ralls, K., D. P. Demaster, and J. A. Estes. 1996. Developing a criterion for delisting the southern sea otter under the U.S. Endangered Species Act. Conservation Biology **10:**1528–1537.

Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. North American Journal of Fisheries Management **21:**756–764.

Ripa, J., and P. Lundberg. 2000. The route to extinction in variable environments. Oikos **90:**89–96.

Sabo, J. L., E. E. Holmes, and P. Kareiva. 2004. Efficacy of simple viability models in ecological risk assessment: does density dependence matter? Ecology **85:**328–341.

Schultz, C. B., and P. C. Hammond. 2003. Using population viability analysis to develop recovery criteria for endangered insects: case study of the Fender's blue butterfly. Conservation Biology **17:**1372–1385.

Snyder, N. F. R., and E. V. Johnson. 1985. Photographic censusing of the 1982–1983 California Condor population. Condor **87:**1–13.

Staples, D. F., M. L. Taper, and B. Dennis. 2004. Estimating population trend and process variation for PVA in the presence of sampling error. Ecology **85:**923–929.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, California.

U.S. Code. 2000. U.S. Endangered Species Act of 1973. 16 U.S. Code Section 1532.

USFWS (U.S. Fish and Wildlife Service). 1994. Whooping Crane recovery plan. Albuquerque, New Mexico.

Zeng, Z., R. M. Nowierski, M. L. Taper, B. Dennis, and W. P. Kemp. 1998. Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. Ecology **79:**2193–2209.