Setting population targets for mammals using body mass as a predictor of population persistence

Jelle P. Hilbers,1,∗† Luca Santini,1,2 † Piero Visconti,3,4 † Aafke M. Schipper,1,5 Cecilia Pinto,6 Carlo Rondinini,2 and Mark A.J. Huijbregts1,5

1Department of Environmental Science, Institute for Wetland and Water Research, Faculty of Science, Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The Netherlands
2Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza Università di Roma, Viale dell’Università 32, 00185 Rome, Italy
4Centre for Biodiversity and Environment Research, University College London, Gower Street, London, WC1E 6BT, U.K.
5PBL Netherlands Environmental Assessment Agency, P.O. Box 30314 NL-2500 GH, The Hague, The Netherlands
6Centre Manche-Mer du Nord, Ifremer, 150 quai Gambetta, BP 699, 62321, Boulogne-sur-Mer, France

Abstract: Conservation planning and biodiversity assessments need quantitative targets to optimize planning options and assess the adequacy of current species protection. However, targets aiming at persistence require population-specific data, which limit their use in favor of fixed and nonspecific targets, likely leading to unequal distribution of conservation efforts among species. We devised a method to derive equitable population targets; that is, quantitative targets of population size that ensure equal probabilities of persistence across a set of species and that can be easily inferred from species-specific traits. In our method, we used models of population dynamics across a range of life-history traits related to species’ body mass to estimate minimum viable population targets. We applied our method to a range of body masses of mammals, from 2 g to 3825 kg. The minimum viable population targets decreased asymptotically with increasing body mass and were on the same order of magnitude as minimum viable population estimates from species- and context-specific studies. Our approach provides a compromise between pragmatic, nonspecific population targets and detailed context-specific estimates of population viability for which only limited data are available. It enables a first estimation of species-specific population targets based on a readily available trait and thus allows setting equitable targets for population persistence in large-scale and multispecies conservation assessments and planning.

Keywords: allometry, conservation biology, conservation target, extinction, minimum viable population, population viability analysis, wildlife, wildlife management

Resumen: La planificación de la conservación y las evaluaciones de la biodiversidad necesitan objetivos cuantitativos para optimizar las opciones de planificación y para evaluar la idoneidad de la protección actual de las especies. Sin embargo, los objetivos con miras a la persistencia de poblaciones requieren datos específicos de población, lo que limita su uso a favor de objetivos fijos y no específicos, lo que probablemente resulta en una distribución desigual de los esfuerzos de conservación entre las especies. Diseñamos un método para derivar objetivos de equitativos de población; esto es, objetivos cuantitativos del tamaño de la población que aseguren probabilidades iguales de persistencia en un conjunto de especies y que puedan ser inferidos fácilmente a partir de las características específicas de la especie. En nuestro método utilizamos modelos de
Introduction

A key goal in conservation biology is the protection of species to ensure stable and viable populations over time (Shaffer 1981). Quantitative conservation targets provide essential benchmarks to design effective conservation actions and evaluate the adequacy of current species protection (Tear et al. 2005; Sanderson 2006; Carwardine et al. 2009). Conservation targets that aim at population persistence can be expressed in terms of the minimum population size to be conserved because population size is a major determinant of wildlife population persistence (Reed et al. 2003; Sanderson 2006). The minimum viable population (MVP) is a long-standing concept in conservation that can be defined as the population size below which extinction risks are deemed unacceptably high (Boyce 1992; Beissinger & McCullough 2002). The MVP is typically quantified on the basis of population viability analyses (PVAs), which are applied to estimate extinction probabilities based on long-term population data on wildlife demographic rates (Akçakaya & Sjögren-Gulve 2000). The MVP estimated through PVA has a certain probability to persist given its current growth rate, which ultimately depends on species’ life-history characteristics and environmental conditions (e.g., habitat, resources, and external pressures). Hence, these MVPs have a short temporal validity, are highly context dependent, and are thus typically inapplicable to other conspecific populations. The applicability of an MVP derived via PVA for setting conservation targets has been questioned because of the limited availability of high-quality, population-specific input data. In fact, MVPs have been calculated for only a limited number of species, often those most studied (Flather et al. 2011).

The need to make rapid decisions about conservation targets for groups of species in large geographic areas has prompted interest in identifying robust, general rules of thumb (Clements et al. 2011). Some authors have recommended the use of a universal target of approximately 5000 individuals to ensure long-term persistence, irrespective of taxonomy, life-history traits, or environmental conditions (e.g., Traill et al. 2010; Brook et al. 2011; Clements et al. 2011). In contrast to the original MVP concept (Shaffer 1981; Shoemaker et al. 2014), this target has been applied at the species level (Clements et al. 2011), regardless of populations’ spatial structure and connectivity (Akçakaya et al. 2011; Beissinger et al. 2011; McCarthy et al. 2011). Species persistence over time is, however, influenced by a number of factors, such as number and size of the populations, connections among them, probability of extinction and colonization events, and distribution of threatening processes. Therefore, persistence targets should be applied at the population level (Di Marco et al. 2016). Estimates of MVP may vary greatly depending on species traits and environmental context; therefore, nonspecific population targets are likely to underestimate adequate protection levels for species that are extinction prone due to their life-history traits and to overestimate adequate protection levels for more stable populations and longer lived species (e.g., Akçakaya et al. 2011; Flather et al. 2011; Garnett & Zander 2011). Wilson et al. (2010) introduced the concept of equitable population targets for conservation, which are population sizes that have the same likelihood of persistence within a given time frame. However, their population targets were estimated using Lande’s (1993) equation of mean time to extinction, which was derived theoretically and not supported empirically and yielded implausible MVP estimates for large species (e.g., approximately 1 Asian elephant [Elephas maximus] and 2 sambar deer [Rusa unicolor] for a 95% survival probability over 100 years [Wilson et al. 2010]).

Body mass has been found to be an important predictor of species vulnerability in its capacity as a good proxy of International Union for Conservation of Nature threat status, probability of extinction, and critical patch size (Cardillo et al. 2005; Hilbers et al. 2016) and has been used to explore conservation trade-offs in reserve-site selection (Kitzes & Merenlender 2013). This is because body mass is a good predictor of a number of life-history

**Palabras Clave:** alometría, análisis de viabilidad poblacional, biología de la conservación, extinción, manejo de vida silvestre, población mínima viable, objetivo de conservación, vida silvestre
traits related to survival, reproduction, and spatial behavior (Savage et al. 2004; Hendriks 2007; Santini et al. 2013). The influence of environmental stochastic effects on animal populations has been related to body mass as well, with larger species being less susceptible to fluctuations in environmental conditions (Sinclair 2003; Hilbers et al. 2016). Given that animal demographic rates and their susceptibility to environmental stochasticity depend on body size, it can be expected that MVP targets are, at least partly, dependent on body size too. However, no one has so far systematically investigated how conservation targets could be tailored to species’ body mass.

We aimed to derive a method to obtain equitable, life-history-informed population targets by developing and implementing allometric relationships for intrinsic growth rate and stochastic effects in models of population dynamics. We applied our method to obtain MVP targets for mammals for which sufficient data were available to derive allometric relationships for demographic parameters. We thus sought to fill the gap between context-specific estimates of population viability and fixed, non-specific population targets for conservation application. Our targets differed fundamentally from MVP estimates based on PVAs because they were context independent in that they were based solely on intrinsic characteristics of the species. As such, as in the original definition of the MVP concept (Shaffer 1981; Shoemaker et al. 2014), the targets were based on the assumption that threats are absent or abated by protection so that the target population has a mean growth rate ≥0 (which is the desired outcome of conservation) that is still fluctuating due to genetic, demographic, and environmental stochasticity. Furthermore, our targets differed from fixed nonspecific targets because they were tailored to species’ biology and were applied at the population level.

Methods

We derived allometric relationships to estimate the maximum intrinsic population growth rate ($r_m$) and its standard deviation ($\sigma_r$) while accounting for their uncertainty. We then used these 2 parameters in density-dependent population dynamics models to obtain equitable population targets for terrestrial mammal species. Finally, we compared these MVP targets with species- and context-specific MVP estimates reported in the literature.

Population Models

It is widely recognized that there is no single best population dynamic model to describe actual population abundance fluctuations in time for all taxa (Brook et al. 2006). Therefore, we used 2 logistic population-dynamic models that are commonly used to describe phenomenological time-series abundance data (Brook et al. 2006):

Ricker logistic,  \[ N_{t+1} = N_t \cdot e^{\left(r_m \left(1 - \frac{N_t}{K}\right) + \sigma_r \varepsilon_t \right)}, \]  (1)

and

Gompertz logistic,  \[ N_{t+1} = N_t \cdot e^{\left(r_m \left(1 - \frac{\ln N_t}{\ln K}\right) + \sigma_r \varepsilon_t \right)}, \]  (2)

where $N_t$ is the population size at time $t$ (in number of individuals), $r_m$ is the intrinsic population growth rate (per unit of time), $K$ is the carrying capacity (in number of individuals), and $\sigma_r$ is the standard deviation of the intrinsic population growth rate $r_m$, thus reflecting the effect of stochasticity on the realized growth rate. The term $\varepsilon_t$ was assumed to represent Gaussian white noise (mean = 0, variance = 1).

Model Parameterization

We used Bayesian inference to estimate $r_m$ and $\sigma_r$ for each body mass while accounting for the uncertainty in the relationships by considering the full posterior distributions of the model coefficients. We collected $r_m$ and $\sigma_r$ estimates and corresponding species’ body masses from Duncan et al. (2007) and Brook et al. (2006), respectively, and fitted linear regression models between log10-transformed $r_m$ and $\sigma_r$ and log10-transformed body mass. The $\sigma_r$ estimates mainly reflected the influence of environmental stochasticity on population growth rate because demographic and genetic stochasticity were not explicitly taken into account by Brook et al. (2006). In a Bayesian framework, prior distributions reflect prior knowledge of a parameter before the analysis. Under Bayes’ rule, prior distributions are modified by the likelihood function to obtain the posterior distribution. Although a negative relationship has been demonstrated for both $r_m$ and $\sigma_r$ with body size (Brook et al. 2006; Duncan et al. 2007), the work that shows this was conducted with the same data sets we used here; therefore, the model coefficients of these negative relationships could not be used to set informative priors. Thus, we used uninformative priors so that the posterior distribution of the parameters was determined by the likelihood function. Prior distributions for the regression coefficients were set according to a normal distribution centered on 0 and with a variance of 31.6 (i.e., $\tau = 0.001$). Similarly, the response variable was assumed to be normally distributed around the mean with a variance following a uniform distribution U(0, 1).
We ran 3 Markov chain Monte Carlo (MCMC) tests of 5000 steps each. We combined the 3 chains and used a thinning parameter of 10 to obtain 2 correlated sets of 1500 posterior estimates of the regression coefficients (intercepts and slope [Supporting Information]). We did not remove the burn-in portion of the chains; rather, we ran 5000 initial iterations for adaptation. Models were checked for parameter identifiability with correlation plots between MCMC chains. The regression coefficients were used to estimate a distribution of \( r_m \) and \( \sigma_r \) for each simulated body mass in the population models (see “Model Parameterization”).

**Model Simulations**

We applied the 2 population models to body masses ranging from 2 g (Suncus etruscus) to 3825 kg (Loxodonta africana), which correspond to the smallest and the largest extant terrestrial mammals, with a numerical simulation optimization routine (300 iterations per body mass). At each iteration, \( r_m \) and \( \sigma_r \) were estimated by sampling the regression coefficients from the MCMC chains (see “Model Parameterization”). This allowed us to account for the uncertainty in the regression estimates and consider a range of possible \( r_m \) and \( \sigma_r \) for each body mass. The initial population size was assumed to be equal to the carrying capacity and thus reflected a situation in which an area was protected to conserve a certain target population size. The initial population size was varied until the species had a 95% probability of surviving for 100 years with an extinction threshold of 2 individuals. We used a time scale of 100 years here because it represents a typical relevant time frame in conservation policy and management (Frankham & Brook 2004; Brook et al. 2006; Shoemaker et al. 2014). We adopted a ceiling in each of the models of population dynamics whereby the population could only increase up to 10% above carrying capacity.

We also ran the simulations with an extinction threshold of 500 individuals to account for stochastic effects other than environmental stochasticity, such as demographic stochasticity, Allee effects, and genetic drift (Franklin 1980; Hilbers et al. 2016). Although our targets were based on the assumption that threats are abated by protection, we also simulated the influence of alleged unfavorable conditions on the MVP targets, which represented habitats of relatively low quality or external factors (e.g., human pressures or predation) that affect the growth rate of species, by applying population growth rates quantified as fractions (80%, 60%, 40%, 20%, and 0%) of the intrinsic population growth rate \( r_m \). The extreme condition of 0% of the intrinsic population growth rate also helped in the interpretation of the relationship between the MVP targets and body mass because in this condition the MVP targets only depended on the standard deviation of the intrinsic population growth rate. The results from the 2 population-dynamic models were averaged to obtain consensus estimates. We derived a consensus model and considered individual population-dynamic models because we wanted to capture the uncertainty in model-derived MVP targets and to obtain a central tendency in MVP-target estimates.

We regressed the log10-transformed MVP targets against log10-transformed body masses and included a quadratic term to account for possible nonlinearity. We used the corrected Akaike’s information criterion (AICc) to identify the most parsimonious models (intercept only, linear, or quadratic). We also compared the resulting regression model estimates for both thresholds and all growth-rate conditions with 135 species- and context-specific MVP estimates for terrestrial mammals (obtained from Brook et al. [2006]). We did this for the MVP targets derived from the individual models of population dynamic and for the consensus estimates. Finally, we derived MVP targets for 5261 terrestrial mammal species from the consensus regression model based on body mass data from Wilman et al. (2014). We derived precautionary MVP targets to account for the uncertainty in the estimates by adopting the upper bound at 2 SD of the estimates (Supporting Information). All analyses were performed in R version 3.1.3 (R Core Team 2014); the rjags package was used for the Bayesian inference (Plummer 2013).

**Results**

The quadratic regression models had the lowest AICc in all cases (Supporting Information) and showed that MVP targets were negatively correlated with body mass (Fig. 1 & Supporting Information). Relationships were nonlinear; MVP targets of heavier species declined less rapidly. Consensus MVP targets based on the intrinsic population growth rate ranged from 9 (3825 kg) to 991 individuals (2 g). Including the influences of unfavorable conditions on the intrinsic growth rates changed the population targets at these body masses to 10–1678 (80% of \( r_m \), 11–4731 (60% of \( r_m \), 14–41219 (40% of \( r_m \), 19–6.26×10^6 (20% of \( r_m \), and 103–7.87×10^5 (0% of \( r_m \). As intrinsic population growth rates decreased, the slopes of the relationships with body mass increased (Table 1). Using an extinction threshold of 500 individuals instead of 2 to account for stochastic effects other than environmental stochasticity resulted in similar slopes but systematically higher intercepts of the relationships (Supporting Information): 2734–6.88×10^5 (\( r_m \), 2934–1.32×10^6 (80% of \( r_m \), 3240–4.18×10^6 (60% of \( r_m \), 3779–3.75×10^7 (40% of \( r_m \), 4523–3.34×10^8 (20% of \( r_m \), and 26,149–8.27×10^17 (0% of \( r_m \). The MVP estimates from Brook et al. (2006) were higher than our MVP targets; approximately 1% of their estimates were below our targets based...
Figure 1. Minimum viable population (MVP) targets in relation to body mass for 6 different intrinsic growth rates ($r_m$) ($80\%$, $60\%$, $40\%$, $20\%$, and $0\%$ of $r_m$) that reflect the influence of low habitat quality or external factors (e.g., human pressures or predation). Targets are based on the consensus model with an extinction threshold of 2 individuals (points, mean of the population target; lines, fit through the mean; whiskers, 2 SD above and below the mean).

on $r_m$, 75% of their estimates were in between our targets based on $r_m$ and 0% of $r_m$, and 24% of their estimates were above our targets based on 0% of $r_m$ (Fig. 2).

Discussion

Interpretation

We combined models of population dynamics and allometric relationships to develop quantitative, body mass-specific conservation targets aiming to ensure population persistence. In contrast to universal targets (e.g., Clements et al. 2011), this approach ensures an equitable distribution of conservation efforts among populations of different species based on the same currency: the estimated probability of persistence.

The MVP targets decreased asymptotically with increasing body mass, in contrast to the results of Traill et al. (2007), who argued that there are no adequate predictors of MVP. Possibly, the signal of body mass in their
MVP targets was masked because they did not control for the effects of anthropogenic pressures and they set MVP at a species-specific temporal scale of 40 generations rather than 100 years (Frankham & Brook 2004). We used a time frame of 100 years because this is a common long-term horizon in conservation policy and management (Frankham & Brook 2004; Brook et al. 2006; Shoemaker et al. 2014). However, we acknowledge that 100 years may be too short to obtain meaningful estimates of population extinction probabilities of longer lived species; therefore, we urge caution in the interpretation of our results for species with long generation lengths (Reed & McCoy 2014).

The relationship we found between population targets and body size reflects the allometric relationship between body size and a population’s susceptibility to environmental stochasticity, which predicts lower susceptibility to environmental stochasticity for larger species. Although larger species also have lower intrinsic population growth rates, which reduces a population’s ability to recover after a decline, the influence of environmental stochasticity becomes so small as body size increases that the probability of severe losses within the time frame of 100 years is greatly reduced. Our results showed this occurred above a body mass of approximately 1 kg; MVP targets of larger species declined much less rapidly than smaller species; this is similar to allometric patterns found by Cardillo et al. (2005).

The comparison with species- and context-specific MVP estimates from Brook et al. (2006) showed that the MVP targets we derived, obtained from relatively simple allometric relationships, are on the same order of magnitude as MVP estimates from species- and context-specific studies. However, our MVP targets were in general lower than the MVP estimates from Brook et al. (2006), especially for mammals larger than 1 kg. This can be explained by the fact that the mean population growth rates of the species in Brook et al. (2006) were in general lower than or close to zero (approximately 45% ≤ 0 and approximately 90% < 0.1), whereas we assumed mean growth rates ≥ 0 (which is the desired outcome of conservation). In addition, the maximum intrinsic population growth rate and its standard deviation of species populations may deviate from the values obtained with the allometric relationships because of trait variability (such as in longevity, generation length, and fecundity) at a given body mass.

A universal target of 5000 individuals to ensure species persistence for at least 100 years, irrespective of taxonomy or life-history traits, has been previously proposed based on meta-analyses of MVP estimates (e.g.,
Traill et al. 2010; Brook et al. 2011; Clements et al. 2011). We have found no support for a universal MVP target, but, according to our findings, 5000 individuals would be sufficient to guarantee the persistence of any population of terrestrial mammal species in habitat of sufficient quality in absence of human impacts or other factors causing deterministic declines. However, 5000 individuals would be largely insufficient for populations of species of <1 kg (majority of mammals) in poor-quality habitat (20% of $r_m$ and 0% $r_m$). Moreover, when we accounted for stochastic effects other than environmental stochasticity, our approach predicted population targets that were consistently higher than a universal target of 5000 individuals for species up to 50 kg. At the other extreme, large species in favorable environments were predicted to require only a small number of individuals to persist for 100 years, which is plausible given the long generation length that characterizes large mammals (Pacifici et al. 2013). These results highlight that in the absence of context-specific MVP estimates, there is added value in differentiating MVP according to body mass.

Application

Our approach provides a coherent way to quantify population targets based on limited data. Our model does not provide an alternative to MVP estimates when sufficient population-specific data are available; rather, it allows one to obtain a first approximation of equitable persistence targets that can be applied to individual populations in multispecies conservation analyses. Our approach thus fills the gap between context-specific estimates of population viability and fixed, nonspecific population targets for conservation application. Given the scarcity of long-term population monitoring data required to obtain population-specific population parameters, we suggest our approach be used to establish tentative population targets for species conservation and recovery programs. In contrast to previously proposed targets for conservation (e.g., Traill et al. 2010; Brook et al. 2011; Clements et al. 2011), our targets should be applied to populations. In large-scale conservation assessments or planning, this can be achieved by focusing on clusters of habitat patches likely interconnected within a species range (Santini et al. 2014; Di Marco et al. 2016; Santini et al. 2016).

When data permit one to estimate a population- and context-specific MVP for a given species, our approach can be used to derive tentative estimates of MVP targets for co-occurring species in order to achieve equitable protection assuming similar conditions. This would allow generating consistent and equitable population targets across populations of different species based on what is known of the environmental conditions in a region, the consequential population dynamics observed for some species, and the body-mass distribution of the species.

For example, the MVP of European bison (Bison bonasus) inhabiting Poland and Belarus is estimated at approximately 250 individuals based on a 95% probability of their surviving for 100 years (Brook et al. 2002). According to our model, a local population of the gray wolves (Canis lupus) inhabiting the same area would then require 352 individuals in absence of human pressures to guarantee its persistence for 100 years. However, our model estimates come with an uncertainty interval that reflects the statistical uncertainty in the allometric relationships and the stochasticity in population dynamics. This does not mean our targets are intrinsically more uncertain than others for which uncertainty has not been quantified. Given the uncertainty in our population targets and the vulnerability of the species, we would opt for applying the precautionary principle and instead adopt the upper bound at 2 SD of the estimates to obtain a population target of 540 gray wolves.

Although species may differ in their response to external pressures, assuming similar conditions and growth potential might be an acceptable simplification in large-scale and multispecies conservation context. Nonetheless, our approach also allows one to assume lower maximum growth rates for a population of a particular species given unfavorable local conditions in order to obtain higher and more risk-adverse targets while assuring equitable protection across species. More generally, depending on local human pressures and the risk-aversion level of managers, the estimates from our models for scaling MVP targets to body mass could be increased to buffer populations against unfavorable conditions, as shown by our simulations assuming low maximum growth rates.

Our population targets can be translated into area targets by multiplying them by the average local population density. Consequently, they can help inform conservation planning algorithms used to design networks of conservation areas that are adequate and efficient (Margules & Pressey 2000; Justus & Sarkar 2002) and address problems of conservation triage (Bottrill et al. 2008). A practical example is provided by species characterized by low density, such as the cheetah (Acionyx jubatus), which has a population density of 0.01 individuals/km$^2$ in well-managed areas and of high-quality habitat (Durant et al. 2015). We estimated an MVP target of 11–14 mature cheetahs, which would require 1400 km$^2$ of high-quality and well-managed habitat to maintain a population for at least 100 years. For 5000 individuals (Traill et al. 2010; Clements et al. 2011), 500,000 km$^2$ (an area the size of Spain) would be needed. When average local population densities are unknown, allometric rules can be used instead. However, we urge caution in doing this because the relationship between population density and body mass may vary by up to 2 orders of magnitude for the same species in different environments (Silva & Downing 1994).
Our relatively simple approach fills the gap between generic and fixed targets for population size on the one hand and data-hungry context-specific estimates on the other hand. It relies on allometric relationships between species life-history traits and body mass that determine species growth rates and its fluctuations and can thus be applied to a wide range of species. Our method accounts for stochastic effects and generation length and allows for adjustments given alleged unfavorable conditions and different precautionary levels. Our estimates can be used in conservation assessments and planning and allow one to optimize resources for conservation by avoiding overinvestment in species that require lower population targets and underinvestment in species that require larger targets.

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Supporting Information

Distribution of the linear regression coefficients sampled through the MCMC chains (Appendix S1), species-specific MVP targets for 5261 terrestrial mammal species (Appendix S2), AICc values for the 3 regression models (intercept-only, linear, and quadratic) (Appendix S3), results of the MVP targets and the comparison with species- and context-specific MVP estimates from Brook et al. (2006) for the Ricker-logistic and Gompertz-logistic population dynamics models (Appendix S4), and results of the MVP targets with the extinction threshold set at 500 individuals (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited


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