

# Estimates of maximum annual population growth rates ( $r_m$ ) of mammals and their application in wildlife management

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## Summary

1. The maximum annual population growth rate ( $r_m$ ) is a critical parameter in many models of wildlife dynamics and management. An important application of  $r_m$  is the estimation of the maximum proportion of a population that can be removed to stop population growth ( $p$ ).
2. When  $r_m$  cannot be estimated in the field, one option is to estimate it from demographic data. We evaluate the use of the relationship between  $r_m$  and female age at first reproduction ( $\alpha$ ), which is independent of phylogeny, to estimate  $r_m$ . We first demonstrate that the relationship between field and demographic estimates of  $r_m$  is unbiased. We then show that the relationship provides an unbiased and simple method to estimate  $r_m$  using data for 64 mammal species. We also show that  $p$  declines exponentially as  $\alpha$  increases.
3. We use the fitted relationship to estimate annual  $r_m$  and  $p$  for 55 mammal species in Australia and New Zealand for which there are no field estimates of  $r_m$ . The estimates differ by species but have low precision (wide 95% credible intervals CIs). Our estimate of  $r_m$  for the Tasmanian devil *Sarcophilus harrisii* is high (0.6, 95% CI: 0.05–2.39) and suggests devils would become extinct if > 0.34 of the population is removed annually (e.g. by facial tumour disease). Our estimate of  $r_m$  (0.77, 95% CI: 0.71–1.05) for brushtail possum *Trichosurus vulpecula* is much greater than published estimates and highlights the need for further field estimates of  $r_m$  for the species in New Zealand.
4. *Synthesis and applications.* Since  $r_m$  has not been estimated in the field for the majority of mammal species, our approach enables estimates with credible intervals for this important parameter to be obtained for any species for which female age at first reproduction is known. However, the estimates have wide 95% CIs. The estimated  $r_m$ , and associated uncertainty can then be used in population and management models, perhaps most importantly to estimate the proportion that if removed annually would drive the population to extinction. Our approach can be used for taxa other than mammals.

**Key-words:** age at first reproduction, Bayesian methods, brushtail possum, conservation, credible intervals, harvesting, rate of increase, Tasmanian devil, uncertainty

## Introduction

The maximum annual population growth rate,  $r_m$ , is the maximum increase in numbers that occurs when resources are not limiting and there are no predators, parasites or competitors (Caughley 1977; Sibly & Hone 2002), although the latter conditions are probably rarely met in the field. The rate  $r_m$  is an important parameter in many wildlife population models, including the logistic (Caughley 1977), generalized logistic (Gil-

pin & Ayala 1973; Sibly *et al.* 2005), ratio (Eberhardt & Peterson 1999) and numerical response (Caughley 1977; Hone *et al.* 2007) models. Estimates of  $r_m$  can also be used to estimate the maximum proportion of a population ( $p$ ) that if removed annually would stop population growth (Caughley 1977; Hone 1999),

$$p = 1 - \left( \frac{1}{e^{r_m}} \right). \quad \text{eqn 1}$$

Annual removals that continually exceed  $p$  will eventually drive the population extinct. The interpretation of  $p$  will

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therefore vary according to whether the wildlife manager wishes to sustain (i.e. threatened or harvested species), or control or eradicate (i.e. pest species) the population. The relationship in eqn 1 was also discussed as the per capita harvest rate needed to stabilize population growth (Slade, Gomulkiewicz & Alexander 1998) and is analogous to the estimation of the threshold proportion of hosts to vaccinate to stop the spread of a disease (Anderson & May 1991).

Estimating  $r_m$  empirically requires reducing a population to low densities under suitable conditions and then estimating population size at standard intervals as the population increases. Maximum annual population growth rate can then be estimated by applying various statistical models to the log-transformed data (e.g. Caughley 1977; Eberhardt 1987; Eberhardt & Simmons 1992). Unsurprisingly,  $r_m$  has not been estimated in the field for the vast majority of species (Duncan, Forsyth & Hone 2007). Researchers and wildlife managers have several options if empirical estimates of  $r_m$  are not available (McCallum 2000). First, they could go into the field and obtain their own estimates, although this is often not feasible for logistic and financial reasons and, for long-lived species, will take some years. Secondly, empirical estimates of maximum population growth rate for a closely related species with similar demographic and reproductive values could be used. Thirdly,  $r_m$  could be estimated from an allometric relationship. Many studies (e.g. Caughley & Krebs 1983; Sinclair 1996) have estimated the relationship between  $r_m$  and body mass ( $M$ ), usually as adult female body mass. Although this can be used to derive estimates of  $r_m$  if body mass is known, the precise form of the relationship is unclear. Thus, while theoretical work predicts an allometric relationship between  $r_m$  and  $M$  with a universal scaling exponent of  $-0.25$  (Savage *et al.* 2004), analysis of data for 294 mammal species (Duncan *et al.* 2007) showed that the actual exponent varied considerably between taxonomic orders, implying that different taxonomic groups require different regression relationships between  $r_m$  and  $M$ .

A fourth option is that  $r_m$  can be estimated from demographic data (e.g. Cole 1954). The advantage here is that we can often derive estimates of  $r_m$ , or make predictions about the relationship between  $r_m$  and other variables, based on established demographic theory (Krebs 2009). Our estimates may therefore have a sound theoretical basis, and we may be able to use what field data we have to test theoretical predictions.

Demographic analysis can use full life-table analysis (Table 1) of age-specific survival ( $l_x$ ) and fecundity ( $b_x$ ) using the Lotka–Euler equation (Caughley 1977; Caswell 2001). The Lotka–Euler equation estimates the growth rate  $r_m$  that occurs with high, constant fecundity rates and low death rates and a stable age structure. However, in many field situations such detailed demographic data are not available and a stable age structure is not attained. A simplification is the two-stage version of the Lotka–Euler equation (Table 1), using juvenile survival ( $l$ ), annual adult survival ( $s$ ), annual fecundity ( $b$ ), age at first reproduction ( $\alpha$ ) and age at last reproduction ( $\omega$ ) (Lande 1988). For estimating  $r_m$ , it is commonly assumed that survival rates approach 1.0 so the equation is reduced to three parameters ( $b$ ,  $\alpha$ ,  $\omega$ ; Table 1) and is the two-stage version of Cole's equation (Cole 1954). This is probably the most widely used equation to estimate  $r_m$  because it is relatively straightforward and requires only three demographic parameters (Slade *et al.* 1998). A different relationship between maximum finite growth rate ( $\lambda_m = e^{r_m}$ ) and age at first reproduction and annual adult survival has been described (Niel & Lebreton 2005), which may be useful when survival rates are available.

Rearrangement of the two-stage version of Cole's equation predicts a negative relationship between  $\log r_m$  and  $\log \alpha$  with a slope of  $-1$  (Table 1). Furthermore, this relationship can be further simplified if we assume that the age at last reproduction ( $\omega$ ) gets very large so that the intercept term is approximated by  $\log_{10}(\log_e b)$ , leading to the following predicted relationship between  $r_m$ ,  $b$  and  $\alpha$  (Table 1):

$$\log_{10} r_m \approx \log_{10}(\log_e b) - \log_{10} \alpha. \quad \text{eqn 2}$$

**Table 1.** Equations and demographic parameters used to estimate maximum annual population growth rate ( $r_m$ ) of mammals

| Equations  | Comments  |
|--|---|
| $\sum l_x b_x e^{-rx} = 1$   | Lotka–Euler equation with age ( $x$ ) classes (Krebs 2009)  |
| $\frac{\lambda^\alpha (1 - (\frac{s}{\lambda})^\omega)}{1 - (\frac{s}{\lambda})^{\omega - \alpha + 1}} = lb$   | Two-stage Lotka–Euler (Lande 1988)  |
| $\frac{\lambda_m^\alpha (1 - (\frac{1}{\lambda_m})^\omega)}{1 - (\frac{1}{\lambda_m})^{\omega - \alpha + 1}} = b$  | Simplified two-stage Lotka–Euler, when $l = s = 1.0$ (two-stage version of Cole's equation)   |
| $\log_{10} r_m = \log_{10} \left( \log_e \left( \frac{b (1 - (\frac{1}{\lambda_m})^{\omega - \alpha + 1})}{1 - (\frac{1}{\lambda_m})^\omega} \right) \right) - \log_{10} \alpha$ | Rearranged version of simplified two-stage Lotka–Euler (achieved by retaining $\lambda^\alpha$ on the left-hand-side and moving all other terms to the right-hand-side, and then taking natural logarithms of both sides of the equation, and then taking logarithms to base 10 of both sides of the equation and rearranging to retain only $\log r_m = \log(\ln \lambda_m)$ on the left-hand-side; see Duncan <i>et al.</i> 2007) |
| $\log_{10} r_m \approx \log_{10}(\log_e b) - \log_{10} \alpha$   | Simplified two-stage Lotka–Euler when $l = s = 1.0$ and $\omega \rightarrow \infty$ . For $r_m > 0$ , then $b > 1.0$  |

Parameters are age-specific survival from birth to age  $x$  ( $l_x$ ), age-specific fecundity ( $b_x$ ), annual fecundity ( $b$  = mean female young/adult female/year), annual adult survival ( $s$ ), survival of juveniles ( $l$ ) from birth to age at first reproduction ( $\alpha$ ), age at last reproduction ( $\omega$ ), maximum annual finite population growth rate ( $\lambda_m$ ) and maximum annual population growth rate ( $r_m$ ).

We have shown that the theoretical slope of this relationship ( $-1$ ) matches empirical data well, and that the slope is independent of phylogeny, which we would expect given that theory predicts a constant (Duncan *et al.* 2007). Hence, the inverse relationship between  $r_m$  and female age at first reproduction ( $\alpha$ ) may provide an even simpler way to estimate  $r_m$ , requiring fewer demographic parameters.

The aim of this paper is to examine how well estimates of  $r_m$  derived from simplified demographic models can predict actual values of  $r_m$  from field count data. This is necessary for managers to assess how useful estimates of  $r_m$  derived from limited demographic data are likely to be when applied to field situations. We evaluate how well Cole's equation (the most widely used method to estimate  $r_m$ ) and the simpler eqn 2 perform in predicting field estimates of  $r_m$ . We then use eqn 2 to predict  $r_m$  for mammal species of pest or conservation concern in Australia and New Zealand for which there are apparently no field estimates, and estimate the annual maximum proportion of a population ( $p$ ) that can be culled, harvested or removed by a threatening process to stop annual population growth. We also estimate  $r_m$  for brushtail possums *Trichosurus vulpecula* Kerr to compare the predicted with a published estimate.

## Materials and methods

### USING COLE'S EQUATION TO PREDICT $r_m$ IN THE FIELD

Duncan *et al.* (2007) reported 33 estimates of  $r_m$  for 17 species of mammals from field count data, where populations were reduced to very low levels and population growth monitored, and where  $r_m$  had been estimated using Cole's equation. Estimates of  $r_m$  from field count data were usually obtained as the slope of the regression of  $\log_e(N_{t+1}/N_t)$  vs. time, where  $N_t$  is abundance (or density) in year  $t$  (Caughley 1977). For some species, there were multiple estimates of  $r_m$  from field count data which varied because maximum rate of population growth in the field will depend on the environmental conditions and available resources at a site, which will differ from place to place. Consequently, there were two sources of variation in  $r_m$  estimates from field count data: within- and between-species. For all but three species, we had a single estimate of  $r_m$  from Cole's equation; for the three species with two estimates, we used the mean. To assess how well Cole's equation can predict values of  $r_m$  estimated in the field, we compared the predicted and observed values by fitting the following model, which partitions the unexplained variation in the field data into between- and within-species components, treating these as random effects:

$$\log_{10}(r_{m \text{ fielddata } ij}) = \beta_0 + \beta_1 \log_{10}(r_{m \text{ predicted from Cole's equation}}) + \theta_j + \varepsilon_{ij}, \quad \text{eqn 3}$$

with  $\theta_j \sim N(0, \sigma_{\text{between-species}}^2)$  and  $\varepsilon_{ij} \sim N(0, \sigma_{\text{within-species}}^2)$ , where  $i, j$  indexes the  $i$ th observation of the  $j$ th species.  $\beta_0$  and  $\beta_1$  are the overall intercept and slope parameters for the relationship between  $r_m$  estimated using field data and  $r_m$  estimated using Cole's equation. The  $\theta_j$  term models differences between species, which are assumed to derive from a normal distribution with variance  $\sigma_{\text{between-species}}^2$ , while  $\varepsilon_{ij}$  is the unexplained within-species variation, also assumed to derive from a normal distribution with

variance  $\sigma_{\text{within-species}}^2$ . If Cole's equation can accurately predict values of  $r_m$  observed in the field, then we expect  $\beta_0$  to be 0,  $\beta_1$  to be 1, and the variance terms  $\sigma_{\text{between-species}}^2$  and  $\sigma_{\text{within-species}}^2$  to be close to 0.

### USING AGE AT FIRST REPRODUCTION AND ANNUAL FECUNDITY TO PREDICT $r_m$ IN THE FIELD

Equation 2 allows us to predict  $r_m$  using annual fecundity data ( $b$ ) and age at first reproduction ( $\alpha$ ), but the double log term in the intercept restricts application of the equation to situations where  $b > 1$  (Table 1). To assess whether the theoretical relationship described by eqn 2 applies, we tested the overall fit of this relationship to empirical data. Duncan *et al.* (2007) reported 98 estimates of  $r_m$  derived from field count data for 64 species of mammals, where estimates of  $\alpha$  were also available. We estimated the intercept term for eqn 2 by calculating mean annual fecundity using data on reproductive output for a large subset of mammals (see below), specified the theoretical slope of  $-1$ , and then compared this relationship with that obtained by fitting a regression line to the data for  $\log_{10} r_m$  vs.  $\log_{10} \alpha$ . If the theoretical relationship holds, then the parameter estimates from the regression model should be close to the theoretically derived slope and intercept.

We estimated mean annual fecundity ( $b$ ) for all mammals using data on litter size and number of litters in Ernest (2003). Annual fecundity (female young per adult female per year) was calculated as (litter size  $\times$  number of litters per year)/2 (i.e. assuming a 1 : 1 birth sex ratio). The data in Ernest (2003) may be biased because certain well-studied mammalian orders are overrepresented in the data (e.g. Artiodactyla and Carnivora) while others are underrepresented. To allow for this, we fitted a model that estimated overall mean annual fecundity with order included as a random effect. We obtained 717 estimates of annual fecundity per female per year for mammals from Ernest (2003), with the overall estimate of mean annual fecundity being  $> 1$ .

In calculating mean annual fecundity, we found substantial variation among orders (see Results). Consequently, when fitting the regression line to the data for  $\log_{10} r_m$  and  $\log_{10} \alpha$ , we included order as a random effect in the regression model, specifying a different intercept for each order as deviations around the overall intercept term. As in eqn 3, we included terms to model both the within- and between-species variation in  $\log_{10} r_m$ .

We fitted all models in a hierarchical Bayesian framework using Monte Carlo Markov Chain (MCMC) methods as implemented in OpenBugs version 2.10 called using the BRugs package from R version 2.6.0 (R Development Core Team 2008). The code is available from the authors on request. All parameters were given prior distributions and we specified non-informative priors to allow the data to drive parameter estimation (McCarthy 2007). The intercept and slope parameters were assigned normal prior distributions with mean 0 and variance 1000. The variance terms were assigned broad uniform priors on the standard deviations following Gelman (2006). The model was run with three chains for 100 000 iterations with a burn-in of 50 000 iterations. Convergence was checked by calculating the Gelman–Rubin convergence statistic (Brooks & Gelman 1988) and by visual inspection of chain-histories to ensure they were well mixed.

### PREDICTION

Mammal species are variously classified as pests, are harvested, or are of conservation concern. Species of conservation concern used here were listed on the website of the Australian government (<http://>

www.environment.gov.au) accessed on 10 March 2010. Species of mammals in New Zealand and Australia for which there are apparently no published estimates of  $r_m$  were identified, so not all listed species are studied here, and subspecies were not differentiated. Data on age (years) at first reproduction of females ( $\alpha$ ) were collated from King (1990, 2005) for New Zealand mammals and Strahan (1995) for Australian mammals. Data for *Rattus norvegicus* are from Burt & Grossenheider (1976). Additional estimates were from Gailard *et al.* (1989) and Ernest (2003). Published estimates of age at first reproduction (i.e. parturition rather than mating) are a mix of the mean age and data on the age of the youngest occurrences of first reproduction. The latter data were selected for use in the present study as we are studying maximum rates of population growth and that occurs under environmental conditions favouring early development and reproduction.

We predicted values of  $r_m$  for these species from the regression of  $\log_{10} r_m$  vs.  $\log_{10} \alpha$ , with the predictions obtained as part of the MCMC procedure. Using this approach, the slope and intercept terms in the regression model were estimated using the data from all 98 observations with values of  $r_m$  and  $\alpha$ , with these slope and intercept terms used to predict  $r_m$  values for those species where only  $\alpha$  was known. An advantage of this approach is that the output is a probability distribution of expected values of  $r_m$  for a given species that incorporates the uncertainties associated with both parameter estimation in the model, and the within- and between-species variation not explained by the model fit. We thus get an estimate of  $r_m$  and its associated uncertainty that reflects the variability likely to be seen in the field, and is therefore of relevance in informing management decisions. We used information on a species taxonomic order to inform  $r_m$  predictions. Thus, when a species belonged to an order for which there was data available to estimate an order-level intercept term in the regression model that information was used to predict  $r_m$ . When a species belonged to an order for which there was no available data, the overall intercept term was used.

Values of  $p$  were also predicted as part of the MCMC procedure following eqn 1. Again, this provided estimates of  $p$  and the uncertainty associated with likely field outcomes. Throughout, we report the means and 95% Bayesian credible intervals (CIs) of parameters.

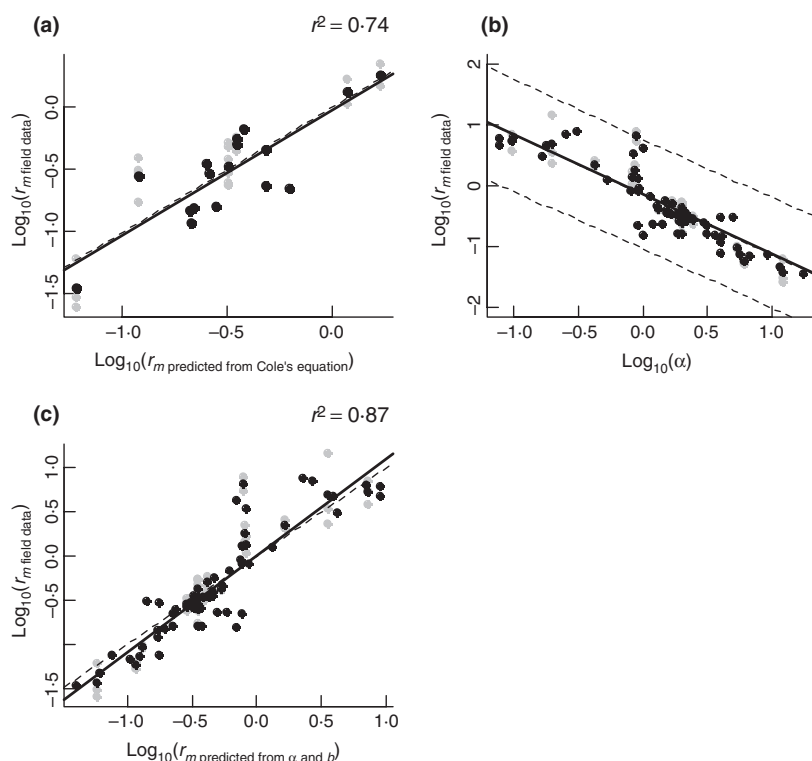
## Results

### USING COLE'S EQUATION TO PREDICT $r_m$ IN THE FIELD

The slope of the linear regression (Fig. 1a) between estimates of  $r_m$  from field count data and from Cole's equation was very close to 1.0 (0.99; 95% CI: 0.62–1.35), with the intercept close to 0 (–0.03; 95% CI: –0.25 to 0.19). The coefficient of determination ( $r^2$ ) was 0.74. The results imply that predictions of  $r_m$  derived from Cole's equation can provide unbiased estimates of  $r_m$  from field count data. Most of the deviations in field values away from the values predicted using Cole's equation were attributed to variation between-species ( $\sigma^2_{\text{between-species}} = 0.052$ ; 95% CI: 0.015–0.127), but there was an appreciable within-species variation ( $\sigma^2_{\text{within-species}} = 0.022$ ; 95% CI: 0.011–0.044), reflecting different field estimates of  $r_m$  for the same species at different locations.

### USING AGE AT FIRST REPRODUCTION AND ANNUAL FECUNDITY TO PREDICT $r_m$ IN THE FIELD

The overall mean annual fecundity, having allowed for variation between orders, was 2.03 female young female<sup>–1</sup> year<sup>–1</sup> (95% CI: 0.71–3.40, with the variation among orders = 5.0, comparable with that within-orders = 6.1). After the double



**Fig. 1.** Relationship between values of  $r_m$  estimated in the field (y axes) and three variables: (a)  $r_m$  estimated using Cole's equation, with the dashed line showing perfect fit and the solid line showing the fitted regression line; (b) age at first reproduction ( $\alpha$ ) assuming a theoretical slope of –1 and an intercept of –0.15 (dotted line, which is hidden) and the fitted regression line (solid). The dashed lines show the 95% CI for predicting the value of  $r_m$  from  $\alpha$  based on the regression fit and assuming the species is from a new order for which there is no data with which to estimate the order-level intercept term; and (c)  $r_m$  estimated from the theoretical relationship with age at first reproduction, assuming a slope of –1 and intercept of –0.15, with the dashed line showing perfect fit and the solid line showing the fitted regression line. Black circles are the mean  $r_m$  values from field data for each species: multiple field estimates for a species are shown as grey dots.



logarithmic transformation in eqn 2, that value equates to an intercept (when  $x = 0$ ) at  $-0.15$  for the relationship between  $\log_{10} r_m$  and  $\log_{10} \alpha$ . Figure 1(b) plots this relationship for values of  $r_m$  observed in the field, with the theoretical (dotted) line overlaid (but difficult to see). The regression line fitted to these data (solid line in Fig. 1b), allowing for variation in the intercept between orders, had an overall intercept at  $-0.16$  (95% CI:  $-0.41$  to  $0.10$ ) and slope of  $-0.99$  (95% CI:  $-1.20$  to  $-0.79$ ), closely matching the theoretical values in eqn 2 of  $-0.15$  and  $-1$ , respectively. Using these theoretical values to estimate  $r_m$  and plotting these predicted values against values of  $r_m$  from field data shows a good fit ( $r^2 = 0.87$ , Fig. 1c). The regression line fitted to these data (solid line in Fig. 1c) had an intercept at  $0.00$  (95% CI:  $-0.08$  to  $0.08$ ) and slope of  $1.10$  (95% CI:  $0.97$ – $1.23$ ), suggesting that the predicted values (dashed line in Fig. 1c) slightly underestimate the observed values for large  $r_m$  and overestimate for small  $r_m$ , although the credible intervals for the slope estimate include  $1.0$ .

#### PREDICTION

The dashed lines in Fig. 1(b) show the 95% CI for values of  $r_m$  predicted from  $\alpha$  using the regression fit and where the species is from an order for which there is no data to estimate the order-level intercept term. There is considerable uncertainty around the predicted values, reflecting uncertainty in parameter estimation, along with the observed variation in field count data, both as deviations in mean species values away from the theoretical value, and variation in values of  $r_m$  for the same species at different locations.

The estimates of annual  $r_m$  of pests and harvested species range from a low of  $0.27$  for alpine chamois *Rupicapra rupicapra* Linnaeus (exotic to New Zealand where it is harvested) to a high of  $4.71$  for *Rattus norvegicus* Berkenhout (exotic to Australia and New Zealand) (Table 2). The estimate of annual  $r_m$  for species of conservation concern ranged from a low of  $0.07$  for southern right whale *Eubalaena australis* Desmoulins to a high of  $6.26$  for eastern barred bandicoot *Perameles gunnii* Gray (Table 3).

**Table 2.** Female age (years) at first reproduction ( $\alpha$ ) and estimates of annual  $r_m$  for mammal species that are pests or harvested in New Zealand and, or, Australia

| Species                    | Order        | $\alpha$ | $r_m$             | $p$              |
|----------------------------|--------------|----------|-------------------|------------------|
| <i>Axis axis</i>           | Artiodactyla | 0.92     | 0.76 (0.21–2)     | 0.49 (0.19–0.86) |
| <i>Axis porcinus</i>       | Artiodactyla | 0.83     | 0.85 (0.24–2.24)  | 0.52 (0.21–0.89) |
| <i>Bos javanicus</i>       | Artiodactyla | 2.13     | 0.32 (0.09–0.84)  | 0.26 (0.09–0.57) |
| <i>Cervus nippon</i>       | Artiodactyla | 1.84     | 0.38 (0.11–0.97)  | 0.3 (0.1–0.62)   |
| <i>Cervus timorensis</i>   | Artiodactyla | 1        | 0.7 (0.2–1.82)    | 0.46 (0.18–0.84) |
| <i>Cervus unicolor</i>     | Artiodactyla | 1.25     | 0.55 (0.16–1.43)  | 0.4 (0.14–0.76)  |
| <i>Dama dama</i>           | Artiodactyla | 1.55     | 0.45 (0.13–1.18)  | 0.34 (0.12–0.69) |
| <i>Rupicapra rupicapra</i> | Artiodactyla | 2.55     | 0.27 (0.08–0.7)   | 0.23 (0.07–0.5)  |
| <i>Canis lupus dingo</i>   | Carnivora    | 1.84     | 0.53 (0.14–1.38)  | 0.38 (0.13–0.75) |
| <i>Felis catus</i>         | Carnivora    | 1        | 0.99 (0.27–2.59)  | 0.57 (0.24–0.93) |
| <i>Erinaceus europaeus</i> | Insectivora  | 0.9      | 1.35 (0.1–5.42)   | 0.55 (0.1–1)     |
| <i>Lepus europaeus</i>     | Lagomorpha   | 0.65     | 1.98 (0.47–5.62)  | 0.77 (0.37–1)    |
| <i>Rattus norvegicus</i>   | Rodentia     | 0.19     | 4.71 (1.27–12.34) | 0.95 (0.72–1)    |
| <i>Rattus rattus</i>       | Rodentia     | 0.25     | 3.57 (0.98–9.33)  | 0.91 (0.63–1)    |

Estimates of  $r_m$  were obtained from the regression analysis (eqn 2). The estimated maximum annual proportion ( $p$ ) of animals to remove to stop population growth is also shown. The 95% credible intervals of  $r_m$  and  $p$  are shown in parentheses.

The estimates of  $p$  ranged from a low of  $0.23$  for *Rupicapra rupicapra* to a high of  $0.95$  for *Rattus norvegicus* (Table 2). The estimates of  $p$  for species of conservation concern varied from  $0.06$  for *Eubalaena australis* to  $0.89$  for *Perameles gunnii* and  $0.94$  for *Notomys fuscus* (Table 3). The uncertainty in estimation generates wide 95% CIs in  $r_m$  and  $p$  values (Tables 2 & 3). Since  $p = 1 - e^{-(0.708/\alpha)} = 1 - e^{-(\ln 2.03/\alpha)}$ , the mean maximum proportion to remove declines rapidly as female age at first reproduction ( $\alpha$ ) increases (Fig. 2a). Species-specific estimates of the annual proportion to remove are shown as a surface in Fig. 2(b).

#### Discussion

Our analysis shows that  $r_m$  estimated from demographic analysis is positively correlated with  $r_m$  estimated independently from field count data (Fig. 1a), a result that gives us confidence in using the demographic analysis to estimate  $r_m$  for other mammal species. The unbiased result contrasts with overestimates of  $r_m$  when using Cole's equation reported by Lynch & Fagan (2009). In the absence of field estimates and demographic data other than female age at first reproduction we recommend that researchers and managers use the relationship between  $r_m$  and  $\alpha$  rather than  $r_m$  and  $M$  (c.f. Caughley & Krebs 1983; Sinclair 1996; McCallum 2000) to estimate  $r_m$  because it is independent of phylogeny (Duncan *et al.* 2007). The variation unaccounted for by the relationship was a result of interspecific variation and we emphasize that the estimates of  $r_m$  (and thus  $p$ ; Tables 2, 3) are the mean for mammal species of a given age at first reproduction. Estimates for individual species could differ due to interspecific variation in annual fecundity, such as lower fecundity of marsupials compared with eutherians (Sinclair 1997).

#### MANAGEMENT IMPLICATIONS

The maximum annual population growth rate is a critical parameter in many population and management models but here we focus on using  $r_m$  to estimate the maximum

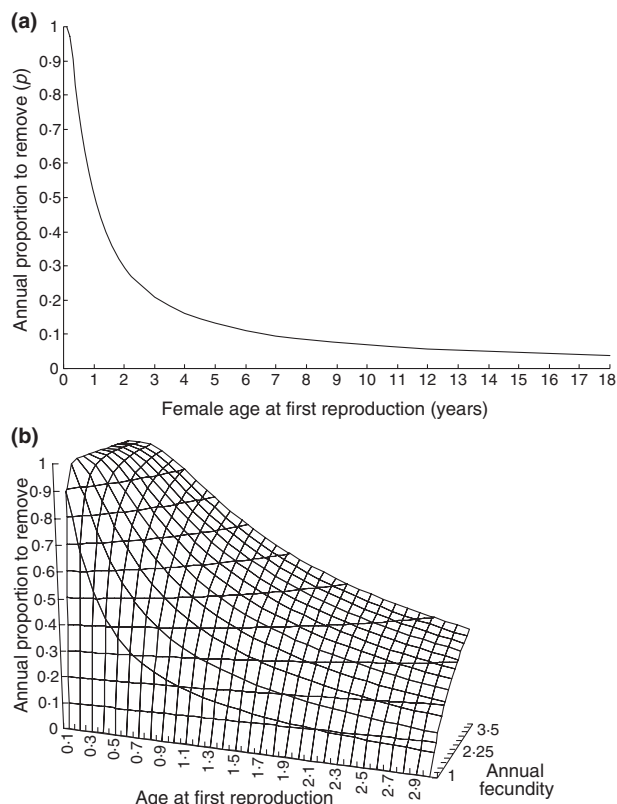
**Table 3.** Estimates of annual  $r_m$  for some Australian mammals that are of conservation concern, for which estimates of female age at first reproduction ( $\alpha$ ) were available

| Species                            | Order           | $\alpha$ | $r_m$             | $p$              |
|------------------------------------|-----------------|----------|-------------------|------------------|
| <b>Endangered</b>                  |                 |          |                   |                  |
| <i>Eubalaena australis</i>         | Cetacea         | 9        | 0.07 (0.02–0.18)  | 0.06 (0.02–0.16) |
| <i>Dasyurus hallucatus</i>         | Dasyuromorphia  | 0.9      | 1.35 (0.11–5.46)  | 0.55 (0.1–1)     |
| <i>Dasyurus maculatus</i>          | Dasyuromorphia  | 1        | 1.21 (0.1–4.84)   | 0.52 (0.09–0.99) |
| <i>Parantechinus apicalis</i>      | Dasyuromorphia  | 0.88     | 1.4 (0.11–5.63)   | 0.56 (0.1–1)     |
| <i>Phascogale calura</i>           | Dasyuromorphia  | 0.9      | 1.34 (0.11–5.39)  | 0.55 (0.1–1)     |
| <i>Sarcophilus harrisii</i>        | Dasyuromorphia  | 2        | 0.6 (0.05–2.39)   | 0.34 (0.05–0.91) |
| <i>Sminthopsis douglasi</i>        | Dasyuromorphia  | 0.42     | 2.91 (0.23–11.99) | 0.75 (0.2–1)     |
| <i>Burramys parvus</i>             | Diprotodontia   | 0.9      | 0.82 (0.21–2.28)  | 0.51 (0.19–0.9)  |
| <i>Gymnobelideus leadbeateri</i>   | Diprotodontia   | 1        | 0.74 (0.19–2.02)  | 0.48 (0.17–0.87) |
| <i>Lagorchestes hirsutus</i>       | Diprotodontia   | 0.9      | 0.83 (0.21–2.28)  | 0.51 (0.19–0.9)  |
| <i>Onychogalea fraenata</i>        | Diprotodontia   | 0.5      | 1.51 (0.38–4.17)  | 0.7 (0.31–0.98)  |
| <i>Potorous longipes</i>           | Diprotodontia   | 2        | 0.37 (0.09–0.99)  | 0.29 (0.09–0.63) |
| <i>Isodon obesulus</i>             | Peramelemorphia | 0.6      | 2.02 (0.16–8.19)  | 0.66 (0.15–1)    |
| <i>Perameles gunnii</i>            | Peramelemorphia | 0.2      | 6.26 (0.46–25.34) | 0.89 (0.37–1)    |
| <b>Vulnerable</b>                  |                 |          |                   |                  |
| <i>Mirounga leonina</i>            | Carnivora       | 3        | 0.32 (0.09–0.84)  | 0.26 (0.08–0.57) |
| <i>Neophoca cinerea</i>            | Carnivora       | 3        | 0.32 (0.09–0.84)  | 0.26 (0.08–0.57) |
| <i>Balaenoptera borealis</i>       | Cetacea         | 8        | 0.08 (0.02–0.2)   | 0.07 (0.02–0.18) |
| <i>Balaenoptera physalus</i>       | Cetacea         | 7.2      | 0.08 (0.02–0.23)  | 0.08 (0.02–0.2)  |
| <i>Chalinolobus dwyeri</i>         | Chiroptera      | 1        | 0.4 (0.08–1.2)    | 0.3 (0.08–0.7)   |
| <i>Pteropus poliocephalus</i>      | Chiroptera      | 2        | 0.19 (0.04–0.57)  | 0.17 (0.04–0.44) |
| <i>Dasyercus byrnei</i>            | Dasyuromorphia  | 0.7      | 1.72 (0.14–6.91)  | 0.62 (0.13–1)    |
| <i>Dasyercus cristicauda</i>       | Dasyuromorphia  | 0.9      | 1.35 (0.11–5.45)  | 0.55 (0.1–1)     |
| <i>Dasyurus geoffroii</i>          | Dasyuromorphia  | 1        | 1.21 (0.1–4.85)   | 0.52 (0.09–0.99) |
| <i>Myrmecobius fasciatus</i>       | Dasyuromorphia  | 1        | 1.21 (0.1–4.83)   | 0.52 (0.09–0.99) |
| <i>Bettongia leueur</i>            | Diprotodontia   | 0.4      | 1.9 (0.47–5.36)   | 0.76 (0.37–1)    |
| <i>Lagorchestes conspicillatus</i> | Diprotodontia   | 1        | 0.74 (0.19–2.04)  | 0.48 (0.17–0.87) |
| <i>Lagostrophus fasciatus</i>      | Diprotodontia   | 1        | 0.74 (0.19–2.03)  | 0.48 (0.17–0.87) |
| <i>Macropus robustus</i>           | Diprotodontia   | 1.6      | 0.46 (0.12–1.27)  | 0.34 (0.11–0.72) |
| <i>Petaurus australis</i>          | Diprotodontia   | 2        | 0.37 (0.09–1.01)  | 0.29 (0.09–0.64) |
| <i>Petrogale penicillata</i>       | Diprotodontia   | 1.5      | 0.49 (0.12–1.34)  | 0.36 (0.12–0.74) |
| <i>Petrogale xanthopus</i>         | Diprotodontia   | 1.5      | 0.49 (0.12–1.35)  | 0.36 (0.12–0.74) |
| <i>Potorous tridactylus</i>        | Diprotodontia   | 1        | 0.74 (0.19–2.03)  | 0.48 (0.17–0.87) |
| <i>Pseudocheirus occidentalis</i>  | Diprotodontia   | 0.83     | 0.89 (0.23–2.43)  | 0.54 (0.2–0.91)  |
| <i>Setonix brachyurus</i>          | Diprotodontia   | 1.1      | 0.67 (0.17–1.83)  | 0.45 (0.16–0.84) |
| <i>Vombatus ursinus</i>            | Diprotodontia   | 2        | 0.37 (0.09–1)     | 0.29 (0.09–0.63) |
| <i>Macrotis lagotis</i>            | Peramelemorphia | 0.4      | 3.06 (0.24–12.59) | 0.76 (0.21–1)    |
| <i>Leporillus conditor</i>         | Rodentia        | 0.6      | 1.47 (0.39–3.87)  | 0.7 (0.32–0.98)  |
| <i>Mesembriomys macrurus</i>       | Rodentia        | 0.83     | 1.06 (0.28–2.82)  | 0.59 (0.24–0.94) |
| <i>Notomys fuscus</i>              | Rodentia        | 0.2      | 4.48 (1.23–11.71) | 0.94 (0.71–1)    |
| <i>Pseudomys australis</i>         | Rodentia        | 0.3      | 2.97 (0.81–7.74)  | 0.88 (0.55–1)    |
| <i>Pseudomys shortridgei</i>       | Rodentia        | 0.9      | 0.98 (0.26–2.59)  | 0.57 (0.23–0.93) |

Species were listed on the website of the Australian government (<http://www.environment.gov.au>) accessed on 10 March 2010. Subspecies listed therein are not discriminated here from species and species are listed here alphabetically within orders. The estimate of the maximum annual proportion ( $p$ ) of animals to remove to stop population growth is also shown. The 95% credible intervals of  $r_m$  and  $p$  are also shown in parentheses.

proportion to remove,  $p$  (eqn 1). The solid line in Fig. 2(a) and the surface in Fig. 2(b) represents threshold levels of annual removals. Above the line, the rate of removals always exceeds the maximum rate of population increase, so abundance must decrease, such that extinction occurs and it is simply a question of when. If the rate of removal varies spatially or temporally, for example with patchiness such that some patches have low removal rates, then control or extinction may not occur. Removals could be through pest control, harvest (recreational, subsistence or commercial), or by predators, parasites or pathogens (as threatening

processes in a conservation sense). The latter set of removals could push a population to extinction if they occur at too high a rate, as shown experimentally (e.g. Hone, Caughley & Grice 2005). The highest value of annual population growth rate is  $r_m$ . Such rates occur very rarely (Sinclair 1997) as shown for rabbit *Oryctolagus cuniculus* Linnaeus, foxes *Vulpes vulpes* Linnaeus and house mouse *Mus musculus* Linnaeus in Australia (Hone 1999). As a result the likely levels of population removals are far lower than estimated here using  $p$  (Tables 2 and 3). Hence,  $p$  is here called the maximum annual proportion to remove.



**Fig. 2.** (a) The relationship between the annual proportion of a population that can be removed ( $p$ ) to stop population growth and female age (years) at first reproduction ( $\alpha$ ), as described by eqn 1. For a given age at first reproduction, an annual removal rate that exceeds the solid line will result in extinction. For a given age at first reproduction, an annual removal rate that is less than the solid line will not result in extinction. (b) Species-specific estimates between the annual proportion of a population that can be removed ( $p$ ) to stop population growth and female age (years) at first reproduction ( $\alpha$ ) and annual fecundity ( $b$ ), for a range of values.

Our analyses treated age at first reproduction ( $\alpha$ ) as a constant. That is a simplifying assumption because  $\alpha$  can vary spatially and temporally with changes in food availability and food quality (e.g. Eberhardt 2002). Changes in  $\alpha$  are predicted to generate changes in the maximum proportion of animals to cull, corresponding to shifts along the  $x$  axis in Fig. 2(a).

Another source of uncertainty is parameter estimation and we accounted for this by using a Bayesian analysis with uninformative priors (McCarthy 2007). An important issue for predictions of  $r_m$  and  $p$  is the choice of credible interval. We chose to estimate 95% credible intervals out of convention, but other intervals may be more appropriate for management situations. For example, there would be an increased probability of eradicating an invasive population if higher values of  $r_m$  and  $p$  (e.g. the upper 95% or 99% credible limit) were used to set harvest (cull) rate, although this would come at the cost of increased effort. Conversely, there would probably be an increased probability of sustaining a threatened population if lower values of  $p$  were used in decision making, although this could increase the cost of managing the process(es) threatening the population. Management decisions may also be more precise if  $r_m$

and  $p$  were estimated from field data for that population and location, but there could be significant financial and temporal costs to doing that. The trade-offs between parameter precisions, cost and management outcome should be evaluated on a case-by-case basis.

The following discussion uses two topical case studies from Australia and New Zealand. The case studies demonstrate the practical application of our approach to wildlife management.

The Tasmanian devil *Sarcophilus harrisi* Boitard is a marsupial carnivore endemic to Tasmania which has been affected recently by facial tumour disease (Hawkins *et al.* 2006; Lachish, Jones & McCallum 2007). Our estimate of  $p$  (0.34; 95% CI: 0.05–0.91 in Table 3) suggests that devils would be unlikely to withstand sustained annual removals  $\geq 0.34$ , however, the 95% CI is very wide. The current high-mortality rate caused by the facial tumour disease (Hawkins *et al.* 2006; Lachish *et al.* 2007), if sustained, could drive affected populations extinct. However, since a small percentage of females first breed at 1 year old (Lachish *et al.* 2007; c.f. 2 years in Table 3 of this study) our estimate of  $r_m$  (0.6) would be biased low if age at first reproduction decreases in response to the disease.

The introduced brushtail possum is an important pest in New Zealand because of its impacts on agriculture (as a host of bovine tuberculosis) and biodiversity (Cowan 2005). The only field-based estimate of  $r_m$  for possums (0.22–0.25) was from faecal pellet counts (Hickling & Pekelharing 1989). Modelling studies used to inform possum control strategies in New Zealand have used estimates of 0.1 [Roberts 1996; criticized as too low by Caley (2006)], 0.2–0.3 (Barlow 1991, 2000) and 0.25 (Bayliss & Choquenot 2002). Our estimate of  $r_m$  of 0.77 (95% CI: 0.71–1.05) is based on a female age at first breeding of 0.92 year (Duncan *et al.* 2007) which suggests that possum populations can increase much faster following control operations than is currently believed. Our analyses suggest that sustained annual removals of  $> 0.54 (= 1 - e^{-0.77})$  of possums are needed to drive populations to extinction. Brushtail possums can, although rarely, breed twice a year with 1.0 young produced in each event (Cowan 2005). An alternative estimate of  $r_m$  can be obtained using equation 27 of Barlow, Kean & Briggs (1997), assuming no deaths;  $r_m = \log_e(1 + 1.0) = 0.69$ , similar to that estimated here (0.77). Our analyses highlight the need for further field-based estimates of  $r_m$  for New Zealand possum populations. McCarthy, Citroen & McCall (2008) show how estimates from allometric relationships can be used to provide objective and informative priors and can be compared with new estimates (e.g. from field studies) in a Bayesian analysis.

## Conclusion

In many situations where  $r_m$  cannot be estimated in the field, or demographic data other than age at first reproduction is lacking, our approach provides an estimate of  $r_m$  that can be used in population and management models, perhaps most importantly to estimate the proportion of a population that if removed on a sustained basis would drive the population

extinct. Our approach can be applied to taxa other than mammals.

However, since estimates of  $r_m$  derived from these relationships may seldom be realized in the field and because of the wide 95% CIs of estimates, a cautious approach should be applied to their use in management.

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