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Human hunting mortality threshold rules for extinction in mammals (and fish)

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ABSTRACT

Question: Are there general life-history rules for exploitation-caused extinction of mammal populations?

Mathematical methods: A population of size N faced with the added mortality of human exploitation will deterministically go extinct if its per-capita birth rate can no longer match its per-capita mortality rate as N approaches zero. We develop exploitation-extinction theory for a mammal life history using $R_0 < 1$ as N goes to zero, and combine the criterion with several facts about mammal life histories.

Conclusions: Extinction results if the ratio of the instantaneous mortality rate caused by hunting (F) divided by the adult instantaneous mortality rate (M, for the unexploited population) exceeds a critical value ($F/M > C$). The C value is determined mostly by the level of recruitment compensation as N declines, and C is likely very similar for different sized mammals. We use existing mammal life-history data to estimate C (~0.5). We then estimate the threshold of instantaneous mortality rate, F, as a function of adult body mass, W; it's a −0.25 power allometry. Finally, we extend the model to fish. C is expected to vary a lot between fish species, mostly because fish are expected to have much larger recruitment compensation than mammals, the recruitment may correlate with body size, and immature fish are often not exploited. We show how to combine these to predict C.

Keywords: exploitation-caused extinction, fisheries-extinction, life span allometry, mammals, population recruitment.

INTRODUCTION

Animal populations may be driven extinct by human exploitation even in the absence of other forms of habitat degradation. This simply requires that the added fishing/hunting mortality overpower the added recruitment normally present as $N \to 0$. Fishery scientists have studied this, theoretically and empirically, for many years (e.g. Myers and Mertz, 1998; Myers *et al.*, 1999; Myers and Worm, 2005). In general, if a fishing fleet exploits several populations

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(stocks) simultaneously, the less productive stocks may well be driven extinct. 'Less productive' is always a combination of low adult mortality rates and poor ability of juvenile recruitment to increase the adult population as N becomes small. In this paper, we build upon – and extend – these deterministic extinction ideas to a mammal-like life history (see also Brook and Bowman, 2005). We use existing life-history data for mammals to produce quantitative rules for extinction in mammals due to over-exploitation. Finally, we discuss how mammals and fish differ.

DETERMINISTIC EXTINCTION THRESHOLD MODEL

An unexploited animal population of size (or density) N_u has birth rates = death rates or, for continuous time reproduction, $b \cdot S_\alpha = M$, where M = adult instantaneous mortality rate, b = daughters produced per mother per unit of time, and S_α = the proportion of b who survive to become reproductive adults at age α. $S_\alpha \cdot b$ is termed the recruitment per adult (or just recruitment), which at N_u equals M as the population is not growing. For simplicity we assume b and M are independent of adult age. We reserve the symbols b and S_α for the b and S values at the equilibrium (unexploited) population size, N_u.

When the population is not at N_u denote the recruitment as S^*b^*. There is much evidence (Fowler, 1981, 1987, 1988; Myers *et al.*, 1999) to support the idea that $S^*b^*$is a declining function of N, while M is independent of N. Thus if we push the population below N_u, S^*b^*will be $> S_\alpha \cdot b$, recruitment will exceed mortality and the population will grow, driving S^*b^*back down to $S_\alpha \cdot b$. As N approaches zero, S^*b^*will approach its highest value, which we shall write as $B \cdot S_\alpha \cdot b$; thus B is the amount we must multiply equilibrium recruitment by to reach maximum S^*b^*at N near zero. We use the symbol B to denote the boost in recruitment as N approaches zero. We leave undetermined whether S or b – or both – show this density dependence (but see below).

The ratios $(S_\alpha \cdot b)/M$ and $(B \cdot S_\alpha \cdot b)/M$ are the average number of daughters (surviving to age α) produced over the adult life span (called the 'net reproductive rate', R_0, by demographers) in the stable and rarified populations, respectively, since $1/M$ is the average adult life span. At N_u, $b \cdot S_\alpha = M$, so $R_0 = 1$. As $N \rightarrow 0$, recruitment $(B \cdot S_\alpha \cdot b)$ rises to its maximum, thus, $R_{0\max} = \dfrac{B \cdot b \cdot S_\alpha}{M} = B$, and $R_{0\max}$ is simply the multiplicative increase in the recruitment per adult as N becomes small.

Now, put the population at N_u and impose an added hunting/fishing mortality with its own instantaneous mortality rate of F. If F falls on all ages, the new total adult mortality rate increases to $M + F$, while survival to α is now decreased by an $e^{-F \cdot \alpha}$ multiplier. R_0 in this newly exploited N_u population is immediately decreased since R_0 now equals $\dfrac{S_\alpha \cdot b \cdot e^{-F \cdot \alpha}}{M + F} < 1$. The population will thus decline, and as it does so recruitment (S^*b^*) will increase. The population will go extinct if the R_0 associated with this exploited population remains < 1 as N approaches 0, or if $\dfrac{B \cdot S_\alpha \cdot b \cdot e^{-F \cdot \alpha}}{M(1 + F/M)} < 1$, which implies:

$$\frac{e^{-\frac{F}{M}\alpha M}}{1 + F/M} < \frac{1}{R_{0\max}}. \tag{1}$$

If F/M satisfies this inequality, the population will deterministically go extinct. Clearly, the threshold F/M, here denoted as C, can be found by solving the following equation:

$$\frac{e^{-C\cdot\alpha M}}{1+C}=\frac{1}{R_{0\max}}. \tag{2}$$

If $C < F/M$, the population is doomed to extinction. Clearly, species with the same $\alpha\cdot M$ and $R_{0\max}$ values have the same C. $\alpha\cdot M$ is known to average about 0.6 in mammals and to be independent of adult body size (Charnov, 1993; Purvis and Harvey, 1995; Fig. 2b shows these 1995 data). $R_{0\max}$ is not known with much precision for mammals, but the data that exist place its central value near 2–3, with no correlation with body size (Fowler, 1981, 1987, 1988). The following argument shows why these small $R_{0\max}$ values are expected for mammals. $S_\alpha\cdot b$ in mammals cannot increase too much, because S_α is already quite high [estimated to be 0.3–0.4 (Charnov, 1993)], and b is expected to be highly dependent upon adult body size, which is not expected to change much as N changes. If b is fixed, $R_{0\max}$ can only reflect the increase in S_α at low N, and the maximum S_α is, of course, one. Probably, maximum S_α is far below 1 (say, 0.6–0.8), rather limiting $R_{0\max}$ to the range of 2–3. Figure 1 shows the extinction threshold, $F/M = C$, for various values of $R_{0\max}$ and $\alpha\cdot M$: the threshold is $C = 0.49$ if $R_{0\max} = 2$ and $\alpha\cdot M = 0.6$, which means if $F/M > 0.49$, species go extinct.

Note again that this extinction rule is a demographic, life-history variable, threshold rule. This will also imply a body size extinction rule since M is, on average, related to body mass (W) in mammals.

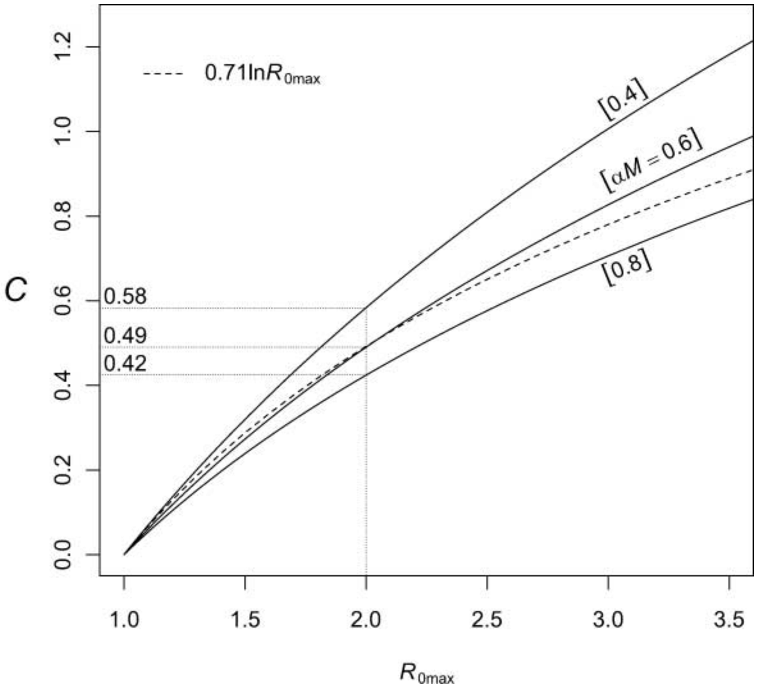

Fig. 1. The F/M critical value (C) for various values of $\alpha\cdot M$ and $R_{0\max}$; at the average $\alpha\cdot M$ of 0.60, $C = 0.49$ if $R_{0\max} = 2$. C is well approximated by $k\ \ln(R_{0\max})$ and the dashed line shows the approximation for $\alpha\cdot M = 0.60$, which makes $k = 0.71$.

Now, suppose all species have the same threshold C: species go extinct if $F/M > C$. Further suppose that M decreases with adult mass, W, according to a quarter power allometry, $\ln M = \ln A - 0.25 \ln W$, where A is a coefficient. Figure 2a shows the most precise data set for mammals (Purvis and Harvey, 1995): $\ln M = -0.38 - 0.25 \ln W$ (units are kg, years). This, combined with $F > 0.49M$, implies that $\ln F > -1.09 - 0.25 \ln W$ is required for extinction, a threshold W for any fixed F; all species larger than the threshold go extinct. Since there is variation in M at any fixed W (Fig. 2a), species with low M at any W may still go extinct even if the average species at that W does not (the reverse applies for species with relatively high M at any W). For example, primates have very low M at any W compared with typical mammals (Charnov and Berrigan, 1993), and thus we expect them to be more prone to extinction at any F and W. Of course, species with low recruitment compensation (equation 1, Fig. 1) are also more likely to go extinct at any F. Elsewhere (Zuo *et al.*, submitted) we have used a version of these rules to help understand the late Pleistocene extinction of mammals.

DISCUSSION

The argument developed here is a continuous time version of similar discrete time arguments used to understand the risk of exploitation-caused extinction in fisheries (Myers and Mertz, 1998; Myers *et al.*, 1999; Myers and Worm, 2005), although in the discrete time versions the final extinction rules are much less transparent than equation (1). Fish differ from mammals in four important ways. First, fish generally have much higher b, or smaller S, which means that the recruitment increase (B) at low N is not restricted to the range 2–3, but can be several times higher (Myers *et al.*, 1999). It really does not matter that b is age/size dependent for fish since the recruitment response can be captured simply with the increase in B (Myers and Mertz, 1998; Myers *et al.*, 1999; Myers and Worm, 2005). However, since exploitation cuts down on the number of older, more fecund individuals, it *may* negatively impact B (called ‘recruitment over-fishing’). Second, the $\alpha \cdot M$ value in equation (1) is ~2 for fish (Charnov, 1993), about three times the mammal value. This decreases C from the mammal value at any fixed $R_{0\mathrm{max}}$ (Fig. 1). Third, not all juvenile fish are available to be caught; equation (1) for a fish exploitation theory where only some of the juveniles are available to be caught simply multiplies the $\alpha \cdot M$ of equation (1) by the fraction of α that includes catchable juveniles. For example, if only the oldest 0.33 of the juveniles can be caught, the exponential term in equation (1) may be written as

$$\frac{e^{-\frac{F}{M}\cdot 0.33\alpha M}}{1 + F/M} < \frac{1}{R_{0\mathrm{max}}}.$$

Fourth, the $R_{0\mathrm{max}}$ ($= B$) value may be larger for larger bodied species, since they generally have larger b, smaller S, and thus have more scope for recruitment to rise as N becomes small.

All of the above combine to make fish extinction rules, both the C values, and the average body size rules more complex. For example, M also declines with W across species of fish (e.g. Charnov, 1993), but since $R_{0\mathrm{max}}$ may rise with W, it is not always clear if large bodied species are expected to be more prone to extinction at any fixed F; it depends upon the balance of these two factors that push C in opposite directions (see Fig. 1). One suspects that larger bodied species *are* more at risk, since the smaller M must generally overpower the larger

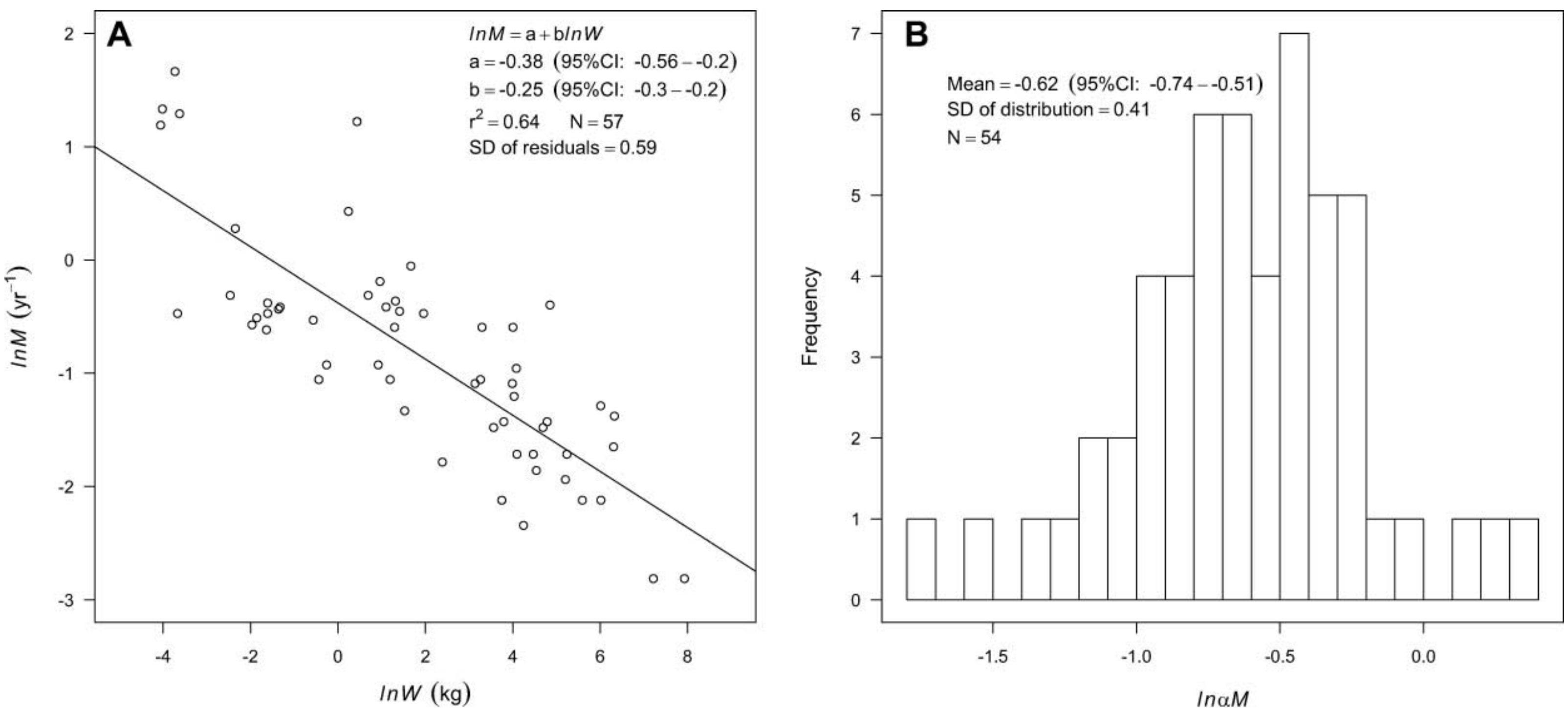

Fig. 2. Adult mortality (M) allometry and distribution of $\ln(\alpha \cdot M)$ for living mammals (Purvis and Harvey, 1995) (excludes bats and primates).

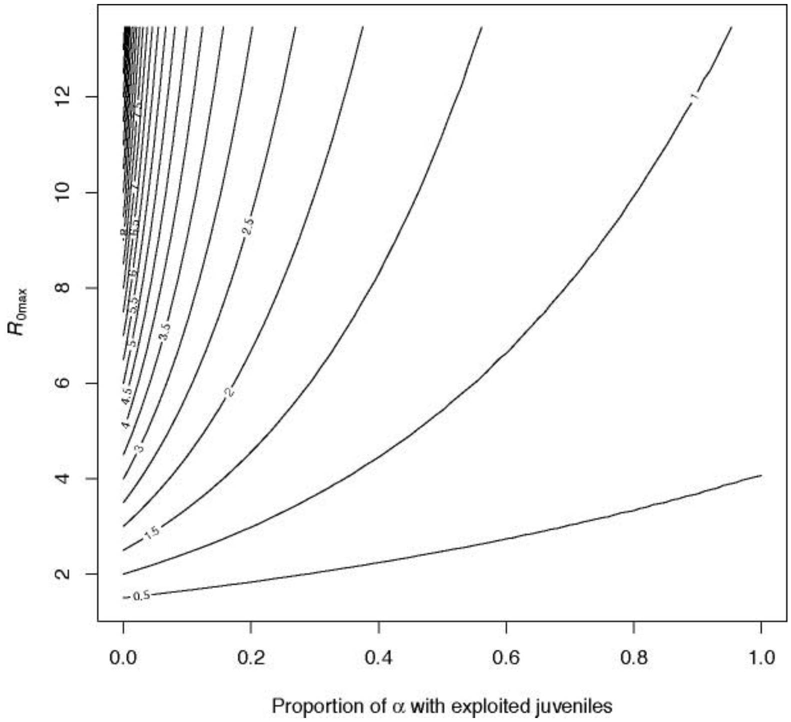

Fig. 3. Fish have R_{0max} values much larger than mammals and juvenile fish are often not exploited in the way that adults are. This figure plots the contours of equal C (F/M threshold) values for these two variables, assuming equation (1) can be used for fish. The C value is rather sensitive to the proportion of non-exploitable juveniles.

ln R_{0max}. Figure 3 shows contours of equal extinction threshold (C) values for various fractions of exploitable juveniles and R_{0max}.

The formalism could be applied to other situations, such as birds on islands; we emphasize mammals simply because the M allometry and other needed numbers are best known for mammals. The formalism might also be useful for other sources of added mortality, such as *new* competitors, predators or disease, perhaps with invasive species. These cases might be more complicated if the added mortality also impacts recruitment or various age classes in ways other than developed here. The formalism probably will not be useful if the impact also degrades the general environment, something common with human impacts; we need to think in terms of F, M or R_{0max}. Of course we have nothing useful to say about community-level impacts of exploitation-caused extinction; individual species formalisms such as equation (1) are mute on things like trophic cascades, and the like.

The extinction criterion used here is equivalent to using F to drive the maximum intrinsic rate of increase (r_{max}) to zero (e.g. Charnov, 1993, equation 6.4b; Brook and Bowman, 2005); clearly, $F = r_{max}$ at its threshold value (if juveniles are fully exploited). The use of $R_0 < 1$ is simply easier than working with the full characteristic equation. For stochastic extinction rules, see Lande *et al.* (2003).

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