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Should hunting mortality mimic the patterns of natural mortality?

Richard Bischof[1,*], Atle Mysterud[2] and Jon E. Swenson[1,3]

[1]*Norwegian University of Life Sciences, PO Box 5003, 1432 Ås, Norway*
[2]*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway*
[3]*Norwegian Institute for Nature Research, 7485 Trondheim, Norway*
**Author for correspondence (richard.bischof@umb.no).*

With growing concerns about the impact of selective harvesting on natural populations, researchers encourage managers to implement harvest regimes that avoid or minimize the potential for demographic and evolutionary side effects. A seemingly intuitive recommendation is to implement harvest regimes that mimic natural mortality patterns. Using stochastic simulations based on a model of risk as a logistic function of a normally distributed biological trait variable, we evaluate the validity of this recommendation when the objective is to minimize the altering effect of harvest on the immediate post-mortality distribution of the trait. We show that, in the absence of compensatory mortality, harvest mimicking natural mortality leads to amplification of the biasing effect expected after natural mortality, whereas an unbiased harvest does not alter the post-mortality trait distribution that would be expected in the absence of harvest. Although our approach focuses only on a subset of many possible objectives for harvest management, it illustrates that a single strategy, such as hunting mimicking natural mortality, may be insufficient to address the complexities of different management objectives with potentially conflicting solutions.

Keywords: demography; life history; simulation; management; selection; vulnerability

1. INTRODUCTION

There is growing concern regarding potential demographic side effects and evolutionary consequences of selective harvesting on wildlife populations (Harris *et al.* 2002; Coltman *et al.* 2003). Perturbations of a population's demographic structure (Mysterud *et al.* 2002; Milner *et al.* 2006) and short- and long-term changes of morphological traits or life-history strategies due to artificial selective pressures (Festa-Bianchet & Apollonio 2003) are some of the processes through which selective hunting may affect populations beyond more obvious, direct effects on population size and growth rate through the removal of individuals. In search of management strategies that minimize the demographic side effects and are 'evolutionarily enlightened' (Gordon *et al.* 2004), it has been suggested that harvesting regimes should mimic natural mortality patterns (e.g. Milner *et al.* 2006; Loehr *et al.* 2007; Bergeron *et al.* 2008). Surprisingly, the general applicability of this recommendation has received little theoretical or empirical evaluation. Recently, Proaktor *et al.* (2007) presented model-based evidence that selection for lighter weight at first reproduction in ungulates could be a consequence of harvest and that harvest pressure is more important in driving this adaptive response than the degree of harvest selectivity. It seems plausible that this would apply to other situations in which the benefits of more and earlier reproduction eventually outweigh its costs (e.g. lower quality offspring), possibly due to higher overall mortality and consequently a greater chance of not reproducing later. To our knowledge, this is the only strong argument thus far in support of the statement that harvest selectivity patterns should mimic natural mortality, because a harvest biased towards younger (and lighter) individuals could minimize the aforementioned adaptive response. Even in such a case, simply targeting small (i.e. young) individuals may lead to further decreases in the size at, and time to, maturation as recent literature on fisheries-induced evolution suggests (Kuparinen & Merilä 2007 and references therein).

In this article, we are specifically concerned about the lack of scrutiny of the statement with regard to the immediate disruption caused due to demographic or other changes as a result of biased harvest. To avoid ambiguity, we identify a clear objective for harvest management with respect to selectivity, namely that harvesting and natural mortality acting on a population should result in a post-mortality population structure (or biological trait distribution) that is identical or at least very similar to the structure that would be expected in the absence of harvest (see also Harris *et al.* 2002). With this objective in mind, we ask the question: should hunting mortality mimic natural mortality in order to limit the potential for disruptions caused by demographic or trait-distribution changes?

The effects of selection on trait distributions are now relatively well understood (e.g. Lynch & Walsh 1998). Particularly relevant to our work is a paper by Vaupel *et al.* (1979), which explores the effects of viability selection on the distribution of a trait over time and age cohorts. The authors termed this trait 'frailty' to highlight the fact that it is related to an individual's risk of mortality, and assumed that the probability density function of frailty follows a gamma distribution. Vaupel *et al.* (1979) further assumed that the force of mortality (a measure of an individual's risk) is a function of time, age and frailty. Although our basic approach is similar, we develop a slightly different model and explore the outcome through the simulations. We also extend Vaupel *et al.* (1979) by discriminating between two mortality causes and by investigating how altering the shape of the viability selection function affects the post-mortality trait distribution.

2. MATERIAL AND METHODS

(a) *Model*

For model construction, we assume a normally distributed random variable x (with mean μ and variance σ) that represents a certain trait of individuals in the population, with associated probability density function

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right). \quad (2.1)$$

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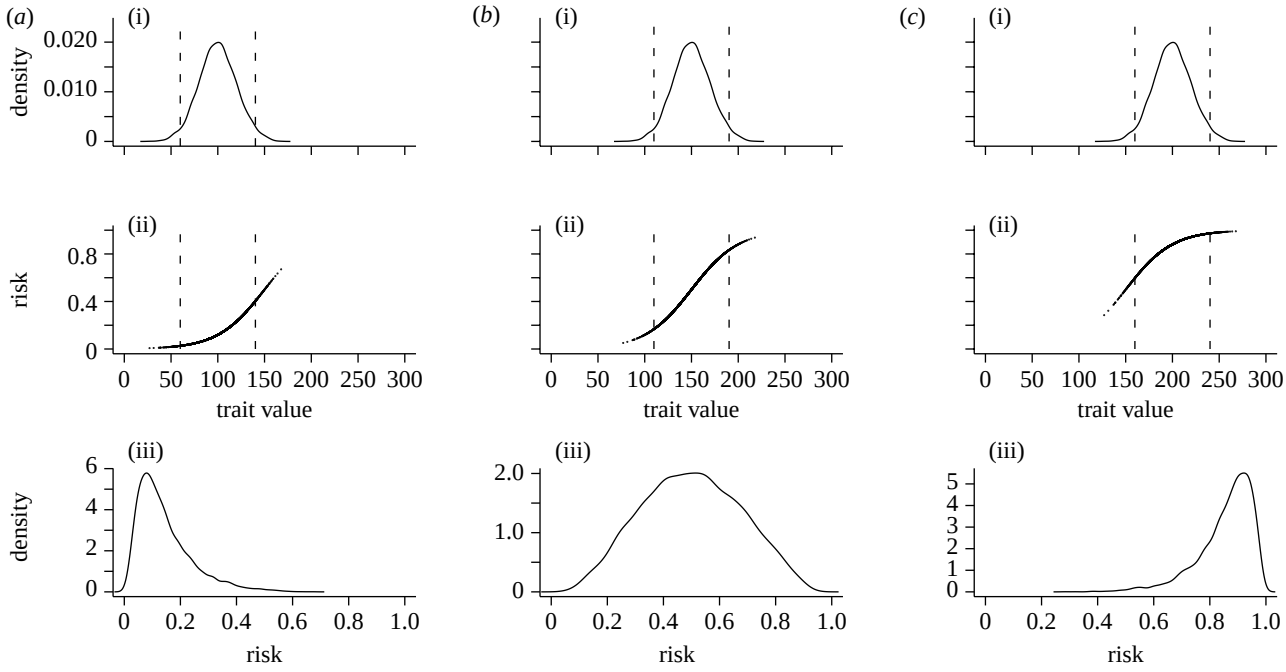

Figure 1. Illustration of the link between the density distribution of risk and a normally distributed biological trait x (s.d. = 20; hashed lines: 2×s.d. boundaries, arbitrary unit), with risk being a logistic function of x. Shifts in the mean trait value ((*a*(i)–(iii)) 100, (*b*(i)–(iii)) 150 and (*c*(i)–(iii)) 200) of a hypothetical population (n = 5000) change the density distribution of risk in the population.

We then assume that risk p is a logistic function of trait x (figure 1), where the relationship between p and x can be expressed as

$$p_x = \frac{1}{1 + e^{-(a+bx)}}. \quad (2.2)$$

Here, a and b are the intercept and slope of the linear regression (with the logit link), respectively. Although the assumptions behind equations (2.1) and (2.2) oversimplify a world where risk probably is a complex function of multiple variables (morphology, age, experience, behaviour, space use, etc.), the approximation is sufficient for our purposes. The above approach centres on a logistic relationship between risk and a normally distributed continuous feature of the population, but this representation also allows the incorporation of discrete or factor variables, as well as other distributions. Following the precautionary principle and because strong compensation can be expected to occur only rarely (Lebreton 2005), we assume that mortality is additive. Furthermore, we ignore potential density-dependent effects that in real populations may, for example, positively affect the growth rate of individuals exhibiting trait values that are selectively targeted.

An interesting finding of Vaupel *et al.* (1979) was that, as individuals age, their force of mortality increases more rapidly than the average force of mortality of the age cohort they belong to, because the removal of frail individuals decreases the average frailty of the surviving cohort. The mechanism underlying this phenomenon applies also to our model, although for simplicity we did not include an age term. While surviving individuals retain their original trait value as they move from pre- to post-mortality, the average trait value shifts towards the less vulnerable end of the trait spectrum (assuming no recruitment within that time step).

(b) *Simulations*

We investigated changes in the probability density distributions of trait x (e.g. size) in a heterogeneous hypothetical population with two groups with different mean trait values (e.g. females and males) resulting from exposure to harvest followed by natural mortality. We evaluated the effect of different shapes of the logistic function linking harvest risk and trait value on both the post-mortality trait distribution and the ratio of the two groups in the population. We used three main expressions of the logistic function based on its shape ('mimic', 'inverse' and 'unbiased'; figure 2) relative to the risk associated with natural mortality, by altering the intercept and slope in the logistic function (equation (2.2)).

We conducted stochastic simulations using R v. 2.5.0 (R Development Core Team 2007). We repeated simulations with the same settings 100 times and calculated bias and 95% CI limits from 1000 bootstrapped replicas of the mean parameter values. We note that, although we chose to illustrate the effect of viability selection using simulations, the effects of multiplying a distribution with a function can also be evaluated analytically, e.g. through the use of conjugate priors within a Bayesian framework (Fink 1997).

3. RESULTS

For the case of harvest preceding natural mortality, simulation results (figure 2, table 1) indicate that (i) inverse harvest risk prior to natural mortality diminishes and in extreme cases reverses the biasing effect of natural mortality on the density distribution of the biological trait, (ii) unbiased harvest risk keeps the biasing effect of natural mortality unchanged, and (iii) mimicking harvest risk amplifies the biasing effect of natural mortality on the density distribution of the biological trait. Biased natural mortality alters the ratio of the two groups in the population, with additional changes in the ratio due to mimic and inverse harvest mortalities, but no further alterations if harvest is unbiased. The altering effect of biased harvest on the trait distribution and the ratio of the two groups in the population increases with increasing harvest rate (table 1). Because we assume no density-dependent effects and, if harvest mortality is limited by a quota, the above patterns, at least qualitatively, also hold true for harvest following natural mortality.

4. DISCUSSION

The general statement that harvest mortality should mimic natural mortality in order to avoid demographic disturbance or evolutionary consequences is not yet sufficiently supported, and needs to be qualified. We found that, for the specific objective of maintaining

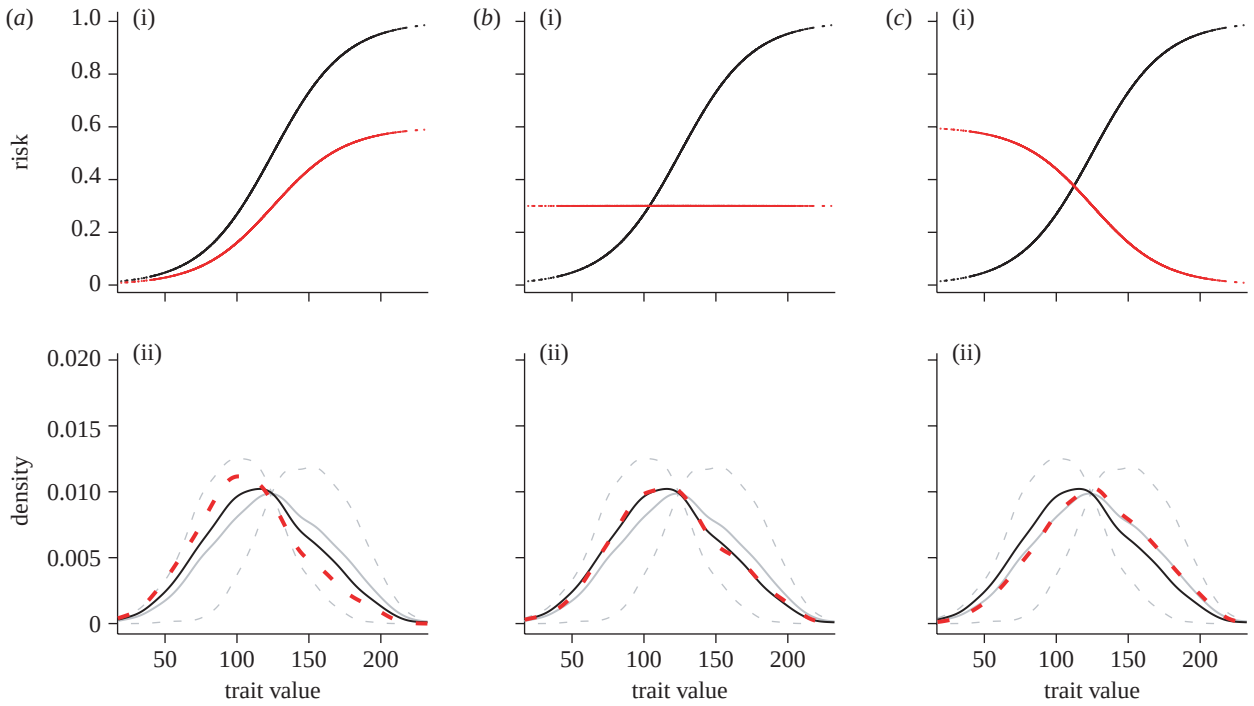

Figure 2. Changes in trait distributions as a result of various patterns of hunting mortality relative to biased natural mortality for a simulated heterogeneous population (two cohorts with $n=1000$ each, s.d.$=30$, 100 and 150). (*a–c*(i)) show natural and hunting risks as a logistic function of the normally distributed biological trait x (arbitrary unit; lines: red, hunting; black, natural). (*a–c*(ii)) show distributions of the biological trait before and after mortality (lines: grey dashed, before mortality (groups separate); grey solid, before mortality (joint); black, after natural mortality without hunting; red dashed, after hunting and natural mortality). Risk associated with hunting mortality either (*a*) mimics natural mortality, is (*b*) unbiased (slope and intercept of the logistic function set to 0), or is (*c*) inverse to natural mortality. Harvest rate was set at 30% of the initial population size.

Table 1. Bootstrapped estimates of the mean trait value (μ, arbitrary unit) and ratio (r) of groups (group 1 : group 2) of surviving individuals in a hypothetical population after hunting followed by natural mortality and after natural mortality in the absence of hunting mortality (μ_0, r_0) from 100 simulation runs for each of the three shapes of the risk function (see text and figure 2) and two different harvest rates. (The initial population consisted of two groups ($n=1000$ each) with mean trait value $\mu=100$ and 150, respectively, and s.d.$=30$. Natural mortality was modelled as a logistic function of x (see text), with intercept $a=-5$ and slope $b=0.04$.)

harvest risk shape	harvest rate	μ	CIL[a] (μ)	μ_0	CIL(μ_0)	r	CIL(r)	r_0	CIL(r_0)
mimic	0.25	103.95	103.82, 104.09	109.12	108.99, 109.25	2.10	2.08, 2.12	1.74	1.72, 1.75
	0.5	96.65	96.52, 96.78	109.05	108.90, 109.20	2.82	2.78, 2.86	1.77	1.75, 1.78
unbiased	0.25	108.92	108.72, 109.12	109.10	108.96, 109.24	1.77	1.75, 1.79	1.75	1.73, 1.77
	0.5	109.14	108.88, 109.38	109.14	109.01, 109.27	1.76	1.73, 1.78	1.74	1.73, 1.76
inverse	0.25	114.47	114.25, 114.70	109.01	108.87, 109.17	1.45	1.43, 1.47	1.77	1.75, 1.78
	0.5	123.97	123.67, 124.25	109.01	108.86, 109.17	1.05	1.04, 1.07	1.75	1.73, 1.77

[a] Ninety-five per cent CI limits from 1000 bootstrapped estimates.

unchanged post-mortality distributions of a trait (or demographic feature), hunting mortality should be unbiased. This holds true regardless of whether hunting occurs prior to or after natural mortality. Therefore, in the absence of strong compensation in mortalities and until further supporting evidence emerges, we would limit recommending that hunting mortality should mimic natural mortality patterns to the following cases.

(i) Natural mortality regimes have been altered, e.g. as a result of extermination of natural predators.
(ii) The objective is to minimize selective pressure for earlier reproduction driven by increased overall mortality as a result of adding harvest.
(iii) An amplification of the biased outcome of natural mortality is desired.
(iv) The main objective is to minimize the negative direct impact of harvest on population growth by targeting those demographic groups whose survival has the lowest elasticity/sensitivity.
(v) Natural mortality is unbiased.

In our example, increasing overall mortality (whether the latter is biased or not) by a constant (e.g. adding unbiased harvest) does not alter the selective pressure on traits directly linked to risk. We emphasize that different objectives, such as (i) minimizing the effects of harvest on the distribution of traits or demographic features or (ii) limiting the selective pressure for lower age and size at first reproduction, may have conflicting solutions, as well as different temporal scopes (see also Law 2001).

We focused on the potential of selective harvest to alter the post-mortality distribution of a single trait from the distribution that would be expected if natural mortality occurred in the absence of harvesting. A wider scope is required to evaluate all important ecological and evolutionary consequences of harvesting and to answer the questions about optimal harvesting strategies comprehensively. Such models may include age effects on trait values and risk, density-dependent effects, and environmental and demographic stochasticity. Furthermore, empirical exploration into how various harvesting strategies in concert with biased natural mortality affect trait distributions of natural populations are required to validate what theory suggests.

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