LETTER

Estimating quasi-extinction risk of European harbour seals: reply to Lonergan & Harwood (2003)

European harbour seal populations have been hit twice by a viral disease resulting in very high mortality rates (Dietz *et al.* 1989; Harding *et al.* 2002). Conjecturing that such mass mortality events can reappear, the long-term effect on population development was explored (Harding *et al.* 2002). Recurrent epizootics were found to substantially increase the probability of a serious decline in population size, a so-called quasi-extinction. There are numerous factors that can be incorporated or left out in modelling quasi-extinction risks. Some of the assumptions tend to decrease the estimated risk, and others to increase it. Lonergan & Harwood (this issue) alter our framework at two points leading to drastically lower estimates of quasi-extinction risk. We argue that a more dynamic approach is necessary. The conclusion of Lonergan & Harwood, that epizootics are 'unlikely to pose serious conservation problems' for the European harbour seal population seems rash.

SAMPLING ERROR AND QUASI-EXTINCTION PROBABILITY

The risk of population declines to a given fraction θ of initial population size is termed the quasi-extinction probability $[P_q(\theta)]$. If the stochastic population growth rate $\log \lambda_s \leq 0$, the population declines so that extinction is certain. If $\log \lambda_s > 0$, the probability that the population declines to the specified fraction can be estimated by:

$$P_q(\theta) = \exp\left(\frac{2 \log \lambda_s \log \theta}{\sigma^2}\right) \qquad (1)$$

(e.g. Lande & Orzack 1988). Based on a time series of population counts from 1979 to 1998, we used the method of Dennis *et al.* (1991) to calculate the maximum likelihood estimate of mean population growth rate ($\log \lambda_s$) to be 0.12 and variance (σ^2) to be 0.06 for the exponential phase of population growth in the Kattegat–Skagerrak (Harding *et al.* 2002). Lonergan & Harwood (this issue) are of the view that our estimate of σ^2 is biased as a consequence of observation errors in the annual counts. Although Lonergan & Harwood are correct in that there is variability in the proportion of the population hauled out on land during surveys, it turns out to be more difficult to correct for this observation error than what they suggest. It is not possible to estimate the sampling error for the entire time series from data for one single year,

and particularly not the year 1988 when the composition of the seal population showed its maximum distance from a stable age structure after the epizootic the same year. Thus, the proportion of seals on land and the variability in this estimate is not constant over the study period (Härkönen *et al.* 2002).

Generally, even if an estimate of observation error can be obtained, it is not clear as to how exactly it should be 'removed' from the estimate of σ^2. The variance term in eqn 1 should reflect both the true variance of the mean stochastic growth rate and the degree of correlation in the time series (Lande & Orzack 1988). Sampling error will tend to increase the variance, but will decrease the overall variance estimate by introducing an anti-correlation among years. This is because annual estimates of growth increments will tend to alternate in size (J.M. McNamara and K.C. Harding, unpublished). How exactly this process is balanced is subject to further analysis (McNamara and Harding, in preparation).

An empirical approach is to study the combined influences of sampling error and epizootics on mean growth rate and its variance in actual data from European harbour seals. In a population, such as the harbour seals in the Wadden Sea, the variance in the mean growth rate is extremely low in non-epizootic periods ($\sigma^2 = 0.002$), and sampling errors can be regarded negligible. Here the quasi-extinction risk $P_q(0.1)$ increases from insignificant levels in the absence of epizootics, to *c.* 0.05 in a situation with epizootics (Table 1). We recalculated the growth rate and its variance for the Kattegat–Skagerrak population using an updated time series 1979–2002. (Population sizes in 2002 were estimated from data on numbers found dead and population growth rate prior to the epizootic.) Although sampling errors are present, they have a minor influence on the $P_q(\theta)$ compared with the large impact of epizootics (Table 1).

IMMUNITY

The inclusion of immunity by Lonergan & Harwoods is a good extension of our framework, as immunity can lower mortality rates in recurrent epizootics. However, Lonergan & Harwood assume that 100% of animals surviving an epizootic are immune. Early analyses after the 1988 phocine

Table 1 Estimated population growth rates among harbour seal populations in Europe. Stochastic growth rate ($\log \lambda_s$), variance (σ^2), and probability for decline to 10% of initial level [$P_q(0.1)$] are given.

Region	Years	Without epizootics			With epizootics		
		$\log \lambda_s$	σ^2	$P_q(0.1)$	$\log \lambda_s$	σ^2	$P_q(0.1)$
K–S	79–02	0.118	0.037	10^{-7}	0.062	0.094	0.05
WS	89–02	0.125	0.002	10^{-161}	0.049	0.077	0.05
Wash	89–02	0.063	0.008	10^{-16}	−0.01	0.074	1
MF	89–02	−0.007	0.013	1	n.a.	n.a.	1

K–S, Kattegat–Skagerrak area; WS, Wadden Sea; Wash, Wash area in England; MF, Moray Firth in Scotland; n.a., not applicable.
Data are based on Thompson *et al.* (2001); Reineking (2002); Reijnders & Brasseur (2003) and this study.

distemper virus outbreak assumed very high levels of exposure to the virus, and homogenous mixing of individuals within the population (Heide-Jørgensen & Härkönen 1992; Swinton *et al.* 1998) seemed to imply high immunity rates of survivors. However, later studies revealed pronounced seasonal segregation of population segments (by sex and age) in harbour seals (Härkönen *et al.* 1999, 2002; Härkönen & Harding 2001). This behavioural trait influences the timing and proportion of different population segments that are infected by the disease (Harding 2000; Härkönen & Harding 2001). Subadult seals are particularly known to escape the disease (Heide-Jørgensen & Härkönen 1992; Thompson *et al.* 1992). Further, serological assays after 1988 showed that only *c.* 50% of the surviving Scottish population had antibodies against the disease (Thompson *et al.* 1992, 2002). We find that reducing the immunity of

Figure 1 Probability of quasi-extinction [P_q (0.1)] depends on the level of immunity among survivors of an epidemic. Mean population growth rate, 0.118 and variance, 0.037 [as estimated from a time series of population counts (1979–2002) from the Kattegat–Skagerrak (Table 1)].

survivors from 100% (as assumed by Lonergan & Harwood) to 50% increases the risk of quasi-extinction fourfold (all other model assumptions kept equal). Thus, the exact rate of immunity among survivors of an epidemic should also be considered in estimating extinction risks for populations that are hit by epidemics (Fig. 1).

POPULATION RATE OF INCREASE

We estimated the $\log \lambda_s$ to be 0.12 for the harbour seal population in the Kattegat–Skagerrak in the absence of epizootics (Harding *et al.* 2002). Lonergan & Harwood assume this rate to be representative for all European populations of harbour seals. However, growth rates among populations vary from the worrying negative values in Scotland and up to 0.125 in the Wadden Sea (Table 1). The mean growth rate has a fundamental impact on estimated extinction probabilities (eqn 1). We plot the quasi-extinction probabilities for a range of population growth rates and variances (Fig. 2). Harbour seal populations in the Kattegat–Skagerrak and the Wadden Sea show high and stable rates of increase, while most other European populations have weaker developments. As epizootics decrease the mean growth rates and increase the variances for all populations, the quasi-extinction probabilities are considerable for many European harbour seal populations (Table 1, Fig. 2).

The models explored by us and Lonergan & Harwood assume that there is no density dependence in the rate of increase. Consequently, we have estimated probabilities for quasi-extinction for the highly unlikely scenario of unlimited exponential population growth. The inclusion of an upper boundary increases the long-term $P_q(\theta)$ to 1 (Middleton *et al.* 1995). To give an example of how a boundary can influence the quasi-extinction risk over a 100-year period, we applied a reflecting boundary at 50 000 individuals for Kattegat–Skagerrak (that is more than twice the pre-epizootic population size in 2002). Under these conditions, the quasi-extinction risk $P_q(0.1)$ increases to 0.09 in the absence of epizootics. With both a reflecting boundary and
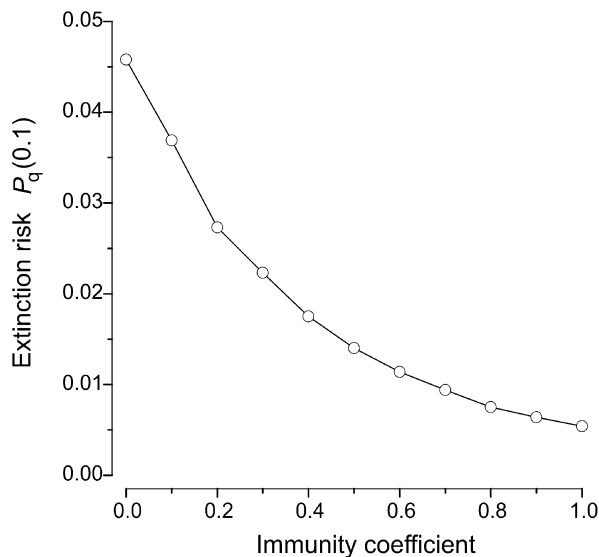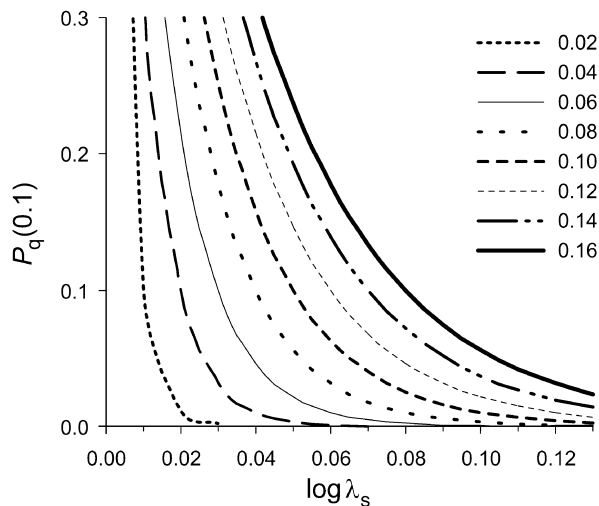
Figure 2 The probability of quasi-extinction [P_q (0.1)] as a function of stochastic growth rate of the population log λ_s (see eqn 1). Values for variances of population growth rates are given by the different lines ranging from 0.02 to the left up to 0.16 to the far right.

epizootics every 14th year, the quasi-extinction risk rises dramatically to 0.56. Obviously, even this mild form of density dependence has dramatic effects on the quasi-extinction risk. For other European seal populations with lower mean rates of population growth and/or lower local carrying capacities, the influence of randomly occurring mass deaths will be even more detrimental (see further Lande 1993).

CONCLUSIONS

In this note we have shown how estimates of quasi-extinction of the harbour seal depend on model assumptions about the exact level of immunity, population growth rate, the variance in population growth and the action of density dependence. Models of quasi-extinction risks are best used as relative tools, where different hypothetical scenarios are compared. However, in this case we can claim that recurrent epizootics with similarly high mortality rates pose a significant risk for severe declines in population sizes and should be taken into account in the management of European harbour seals.

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