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Selective harvesting with equations: comment on 'Should hunting mortality mimic the patterns of natural mortality?'

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Comment

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There is an increased interest in the effects of hunting on the genetic structure of populations, and the distribution of important phenotypes, such as size and horn growth (e.g. Coltman *et al.* 2003; Kuparinen & Merilä 2007). This raises questions about how to maintain hunted populations, and how we should maintain variation in important traits, such as those that are desired by hunters. Recently, Bischof *et al.* (2008) have asked how hunting effort should be distributed across a trait. They suggested that a good strategy should lead to a post-mortality, post-harvest distribution that was identical to the post-mortality distribution. They generalized from a small number of simulations to conclude that the strategy that would meet this goal would be one where hunting was evenly distributed across the trait. This raises several questions: why do we want to mimic natural mortality? How general are the results? How easy is it to carry out a uniform hunting strategy?

The generality problem is a technical one. Bischof *et al.* (2008) have used only a small range of parameters and models to infer their conclusion. But it is simple to show mathematically that their result holds for arbitrary traits and selection. We can assume that the distribution of the trait x has a probability density $f(x)$ before selection, $f'(x)$ after mortality selection but before hunting and $f''(x)$ after both mortality selection and hunting. The effect of mortality is to kill an individual with trait value x with probability $s(x)$, and hunting kills an individual with trait value x with probability $h(x)$. The criterion of Bischof *et al.* for a good hunting strategy is the one that leaves the distribution of the trait unchanged, i.e. $f'(x) = f''(x)$. What hunting strategy will lead to this?

From the basic probability theory and the action of selection described above, the (probability) distribution of the trait after selection is

$$f'(x) = \frac{s(x)f(x)}{\int s(x)f(x)\mathrm{d}x}. \quad (1)$$

The denominator is just a normalizing constant (to make the total probability equal to 1). Similarly, the distribution of the trait after selection and harvesting is

$$f''(x) = \frac{s(x)h(x)f(x)}{\int s(x)h(x)f(x)\mathrm{d}x}. \quad (2)$$

The accompanying reply can be viewed on page 213 or at http://dx.doi.org/doi:10.1098/rsbl.2008.0751.

Again, the denominator is a constant. For optimal harvesting, we require $f'(x) = f''(x)$, i.e.

$$\frac{s(x)f(x)}{\int s(x)f(x)\mathrm{d}x} = \frac{s(x)h(x)f(x)}{\int s(x)h(x)f(x)\mathrm{d}x}. \quad (3)$$

Or, after rearrangement,

$$h(x) = \frac{\int s(x)h(x)f(x)\mathrm{d}x}{\int s(x)f(x)\mathrm{d}x}, \quad (4)$$

i.e. a constant (as both the numerator and denominator are constants). Hence, for an arbitrary trait distribution and selection, the result holds that hunting mortality, which is independent of the trait, will leave the distribution of the trait unchanged. Note that the order of selection and harvesting is not important. It is also clear that the other results of the authors generalize: if we think of hunting as being skewed towards lower trait values, it is easy to see that this will decrease the mean trait value from the no hunting/even hunting scenario.

This result still holds if the hunting is distributed in time, e.g. if the trait is age. In this case, there may be multiple rounds of selection and hunting, but after each round the trait distribution will be unchanged and hence (by induction), there will be no overall change in the trait distribution, i.e. the age profile of the population.

Even if we are happy that a uniform hunting effort will not change the post-harvesting distribution, it is not clear if this is the correct distribution to aim for. Bischof *et al.* only state that the target is unambiguous. They are aiming to mimic natural mortality, but what is meant by natural is not clear, either in general (e.g. Siipi 2004) or in this context (because hunted populations are in contact with humans, and so are undoubtedly influenced in other ways as well).

A more subtle problem is that targeting a non-harvesting distribution ignores any dynamics. For example, the effect of hunting will be to reduce the total population size, and this may lead to compensation and environmentally induced changes in the trait distribution in subsequent years. For example, if density differentially affects differently aged individuals (e.g. Forchhammer *et al.* 2001) uniform harvesting will change the trait distribution. Hunting may also affect reproduction: altering the distribution of the trait (e.g. ornaments such as horns and antlers) may also alter the breeding successes of the surviving individuals, causing a further change in the trait distribution. Increased mortality may thus alter the distribution of the targeted trait through knock-on effects in other parts of the life cycle.

Even if we can satisfactorily define the target distribution, controlling hunting to achieve this may be difficult. Hunting is selective, in one way or another (e.g. Law 2000), and achieving a uniform hunting effort across a trait seems difficult to maintain, especially if the trait is one that is important for hunters, such as size. Changing hunting pressures is possible, but effective strategies are not precise (e.g. limiting mesh size in nets or changing the hunting season), so the effects will probably be crude. Perhaps then, relatively simple models for hunting selection are all that are needed: any refinements will have a minor impact in comparison with the messiness of the effect of any practical recommendations.

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