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Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example

Hanna Kokko

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The sustainability of exploitation is based on density-dependent renewal of populations: when population density decreases as some individuals are taken, the remaining individuals compensate by surviving or reproducing better. In general there is a trade-off between two desired outcomes: a high yield and a high remaining population size. A hunting strategy is Pareto optimal if it balances this trade-off without wasting possibilities of improving the performance in either aspect. Lack of knowledge concerning the age structure, mating system or density dependence operating in a population will very easily cause suboptimality in this sense, whereas utilising knowledge of density dependence may, in some cases, even overcome the conflict between the goals, so that harvesting can increase rather than decrease population sizes. Suboptimal timing of harvesting is an example which not only causes unnecessary harm to a population, but also hampers estimation of the compensatory or additive nature of mortality. A bias towards additivity will be found if hunting and natural mortality overlap in time, and even 'superadditive' results are possible. A mortality pattern that appears additive cannot, therefore, be used to deduce that overwinter survival is density independent. These results have consequences to harvest planning. Adjusting the length of the open season is a tool frequently used to regulate the harvest. Since estimated slopes of compensation cannot be assumed to remain constant if the timing of the open season is changed, the effect of a prolonged season will be more drastic than a mere change in kill rates would predict. Such factors are likely to have the strongest effects in species with long harvest seasons, such as many migratory European waterfowl.

Key words: additive mortality, compensatory mortality, density dependence, seasonality, spring hunting, trade-offs, yield

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The concept of sustainable harvesting is fundamentally linked to density-dependent responses of populations to exploitation (e.g. Getz & Haight 1989, Clark 1990a, Milner-Gulland & Mace 1998). In a density-dependent setting, a population at equilibrium (at its carrying capacity) experiences no net growth, whereas less dense populations have a tendency to grow. In other words, the population is observed to compensate for a loss in numbers by enhanced reproduction or survival of the remaining individuals. Exploiting a population that is originally at equilibrium will therefore reduce the population density until a point is reached where net growth equals the harvest levels; at this point, it is possible to sustain a harvest without further reducing population sizes. The required density reduction is greater for larger harvests (see Fig. 1), which implies a trade-off between two generally desirable goals: a large yield and a minimal reduction of population density. The former goal is obviously of interest to hunters. The latter is of interest to hunters and conservationists alike, as the

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persistence of too small populations may become threatened, thereby also precluding plans to carry on current hunting practices in the future. The decision of a manager is to balance these two opposite preferences.

In many respects, the above view is an oversimplification. Firstly, it is not always clear that maintaining a maximally large population is a desirable aim. For example, too dense deer populations can cause damage such as overgrazing or road accidents (Putman 1997, Putman & Moore 1998), and since some hunted species are considered pests, their (local) extinction may even be desirable (Hone 1994). Secondly, it ignores stochastic variation in population sizes (Sæther, Engen & Lande 1996) and the dynamics of unstable populations such as those exhibited by cyclic populations of many gamebirds (Hudson 1992, Lindström 1994). Both kinds of population fluctuations have profound implications on optimal management of populations (e.g. Engen, Lande & Sæther 1997, Lande, Sæther & Engen 1997, Hudson & Dobson 2001). When stochasticity is present, the goal of maintaining a healthy population indefinitely has to be replaced with a probabilistic criterion, such as a preference for a maximally long extinction time (Engen et al. 1997).

Harvesting in temporally varying populations is treated elsewhere in this issue (Sæther, Engen & Solberg 2001, Hudson & Dobson 2001), and pest control is not included in the current scope of sustainable harvesting, as sustainability is not desired in that case. Here, I concentrate instead on other ways in which management decisions may deviate from the simple setting of a trade-off as laid out above. I also utilise the concept of Pareto optimality (Bunn 1984) to distinguish between strategies that are clearly suboptimal and those that do make full use of the unavoidable trade-offs in population management.

In decision-making theory (Bunn 1984), decisions that take multiple (and partly incompatible) preferences into account are considered 'Pareto optimal' if the strategy's performance according to one criterion could not be improved upon without compromising the performance in another respect. A non-Pareto optimal strategy, on the other hand, causes a deviation from one of these goals, which could have been avoided given a desired degree of fulfilling another goal. In the context of harvesting, suboptimality means causing unnecessarily much harm to a population, in terms of reduced population density or a measure of persistence, when harvesting a specific yield. I argue here that such suboptimal decisions are potentially very common in management practices, that they can often be related to lack of information, and that, unfortunately, suboptimal management strategies themselves can hamper the attempt to gather more information.

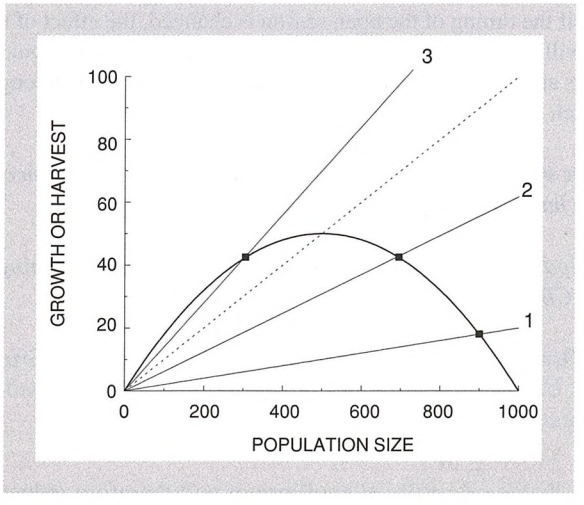


Figure 1. Pareto optimality in the context of harvesting. Up to a point, reducing the population from its equilibrium size (here 1,000 individuals) causes stronger net growth, which can then be removed by harvesting. To the right of the dotted line, larger reductions in the population size always correspond to larger yields, as is exemplified by comparing hunting efforts 1 and 2. In a setting where the preferences of management are to minimise the reduction in population size and maximise the yield, both efforts (and, indeed, any effort right to the dotted line) are Pareto optimal: the performance according to one criterion cannot be improved without compromising the other. By contrast, effort level 3 is suboptimal, as it causes a drastic decrease in population size compared to effort level 2, without any improvement in the yield.

Suboptimal harvesting

The most fundamental blunder that a manager can make to cause non-Pareto optimality is undoubtedly overexploitation. In Figure 1, strategies 1 and 2 are both Pareto optimal: hunting effort 1 gives a lower yield but spares more of the population, compared to the effort marked with 2. The choice between these two is a matter of how much weight an individual manager places on these two opposing values, and optimality theory does not comment on their relative superiority. However, using effort level 3 instead of level 2 is a clearly suboptimal choice: the population size becomes now markedly reduced, without any improvement in yield. Indeed, any hunting effort larger than the dotted line (see Fig. 1) is non-Pareto optimal, as it is inferior to a strategy which would allow the same yield to be taken on the lower right side of the line that passes through the maximum sustainable yield (MSY; see Fig. 1). It can be noted that the usual arguments against the usefulness of the MSY concept (Ludwig, Hilborn & Walters 1993) do not affect this conclusion, as the increasing threat to the

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population as the MSY is approached can be simply seen as an indication of a deviation from the conservationist's goal of keeping the population size large. One should remember, however, that environmental stochasticity can strongly influence the MSY (Sæther et al. 1996), and hence the point at which strategies become suboptimal.

The suboptimality of overexploitation is very well recognised in the management literature of both marine and terrestrial populations (e.g. Royce 1987, Getz & Haight 1989, Ludwig et al. 1993, Taylor & Dunstone 1996), but the implementation of the simplest solution - exploitation at a lower rate - is often hindered by economic, social and political problems (Hardin 1968, Caughley 1993, Ludwig et al. 1993, Sutherland & Reynolds 1998). Here, I will instead consider more subtle ways in which harvesting may cause too much harm to a population. It is not hard to imagine settings where, even if management was carefully planned and problems of shortsighted overexploitation could be avoided, hunting would not be fully optimised because of incomplete data on population size or structure. The basic reason for this is that populations are rarely homogeneous collections of individuals. Whenever individuals differ in their contribution to population growth, removing individuals randomly will be inferior to a more carefully planned harvesting strategy.

For example, if density dependence operates mainly through decreased juvenile survival at high population densities, a young animal may be part of a 'doomed surplus' (Errington 1934), meaning that it could be killed without any adverse effects on population productivity. Sparing this juvenile and killing an adult female instead would then be a suboptimal decision: the productivity of the population is decreased, but the yield is not improved (though this obviously depends on body sizes of adult and young individuals and their possible values as trophies). But the opposite scenario is also possible: old individuals approaching senescence may have lower reproductive values than juveniles approaching maturity, and in that case it would make sense to kill the older individual (see also Law & Grey 1988, Kokko, Lindström & Ranta 2001). Therefore, avoiding suboptimal decisions requires knowledge on age-dependent survival and fecundity parameters, and their responses to population density. Deriving sensitivities of population growth to changes in life-cycle transition probabilities is often used to guide management decisions in such cases (Benton & Grant 1999). Such models, however, have to be used with care as sensitivity to changes in a certain matrix element do not directly translate to impacts when killing one individual (de Kroon, van Groenendael & Ehrlén 2000, Kokko et al. 2001). Also, matrix models very rarely incorporate density dependence, even though the sustainability of the harvest relies on this very phenomenon (though see e.g. Alvarez-Buylla 1994).

Another clear example where lack of information will prevent complete optimisation is sex-specific harvesting. It often makes sense to cull males instead of females, as their contribution to population growth is to a great extent replaceable by the remaining males in the population (Ginsberg & Milner-Gulland 1994, Lindström 1998). Especially if males compete for the same resources with females or indeed harm female reproduction by sexual harassment (e.g. Reale, Bousses & Chapuis 1996), achieving a female-biased sex ratio could greatly improve population productivity. In such settings, it is suboptimal to harvest while not biasing the sex ratio to the extreme, where further biasing would make population growth plummet because of lack of males. Yet, maintaining a minimal stock of males that are still capable of fertilising the female population would require information on the breeding system at extremely biased and not naturally occurring sex ratios (Kokko et al. 2001). It is clear that this means either very courageous extrapolation of biological knowledge, or very courageous experiments. A more cautious approach is to avoid extreme biases, yet this automatically means that the yield taken will be reducing the population more than necessary.

Lack of knowledge of factors such as age-specific survival, density dependence and the relationship between the sex ratio and female fecundity, may thus easily thwart plans to harvest in a way that would avoid mistakes in the sense defined above. I will now proceed to show that the problem of gaining enough information extends to the other direction: a misjudged harvesting strategy may in fact lead to a bias in the information we collect from a population, thus making it more difficult to detect the true effects of harvesting.

Timing of harvest

It is increasingly recognised that the timing of harvesting may profoundly influence the impact on the population (de Gee & Grasman 1998, Kokko & Lindström 1998, Kokko, Pöysä, Lindström & Ranta 1998, Jonzén & Lundberg 1999, Boyce, Sinclair & White 1999, Hudson & Dobson 2001). The basic reason for this is that in seasonal environments, reproduction and (most of) mortality tend not to coincide in time, and this leads to annual fluctuations in population size. Consequently,

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removing an individual just prior to reproduction (spring harvesting) causes a larger reduction in the population than if the individual had been removed earlier (autumn harvesting). In the latter case it could have died in any case before ever reproducing again, and this reduces its expected contribution to population growth (see also Doubleday 1975).

Furthermore, when mortalities are density dependent, population responses to timing of harvesting can be even more dramatic. In such cases a manager who does not know the density-dependent structure of the population may miss real opportunities to make good use of trade-offs. This can be illustrated by considering two scenarios for density-dependent mortality during the winter. In the first scenario, daily mortality, $\mu(t)$, is a function of the current population size, $x(t)$, where t denotes the fraction of the winter that has passed. Daily mortality rate thus decreases as the number of competitors dwindles during winter. In the second scenario, daily mortality is assumed constant throughout the winter, and it is instead determined by environmental conditions at the start of the winter: the larger the population at that time, the higher the mortality. Assuming linear relationships between mortality and population size and density-independent reproduction in both of these cases, Kokko & Lindström (1998) derived expressions for the population dynamics for the whole year. The first case brings about Beverton-Holt population dynamics (Beverton & Holt 1957), described by $x(t+1) = \lambda_0 x(t) (1+\mu_0 x(t))^{-1}$, while the second case corresponds to Ricker dynamics (Ricker 1954), $x(t+1) = \lambda_0 x(t) e^{-\mu_0 x(t)}$ (λ_0 and μ_0 being parameters for fecundity and mortality, respectively).

How much difference does the timing of harvesting make in these two cases? A simple numerical example is given in Figure 2, where a population with parameters $\lambda_0 = 5$, $\mu_0 = 0.005$ is subjected to a total annual kill of 50 individuals. In the Beverton-Holt case (see Fig. 2A), harvesting in the autumn has an almost negligible impact on the population (a reduction in the post-breeding population size from 800 to 786 individuals), whereas a spring harvest of the same size causes a reduction of almost 50% (from 800 to 435 individuals). The Ricker dynamics (see Fig. 2B) is even more sensitive to the harvest timing. Spring harvest of 50 individuals drives the population extinct, whereas autumn harvesting increases the equilibrium post-breeding population size by 6% (see Fig. 2B). This happens because the Ricker density dependence is overcompensatory, as indicated by its decreasing slope at high population densities. The population size at the start of the winter has such a strong influence on subsequent mortality that, up to a point, reducing the number of individuals that enter the winter phase will increase the number of individuals surviving it (assuming that harvesting occurs soon enough to make the environment more favourable for the remaining survivors; see Kokko & Lindström 1998). Equipped with knowledge of seasonal density dependence, a manager could, if lucky enough to encounter a population that obeys dynamics as described above, attain both of his goals: simultaneously increase the yield and the remaining population size.

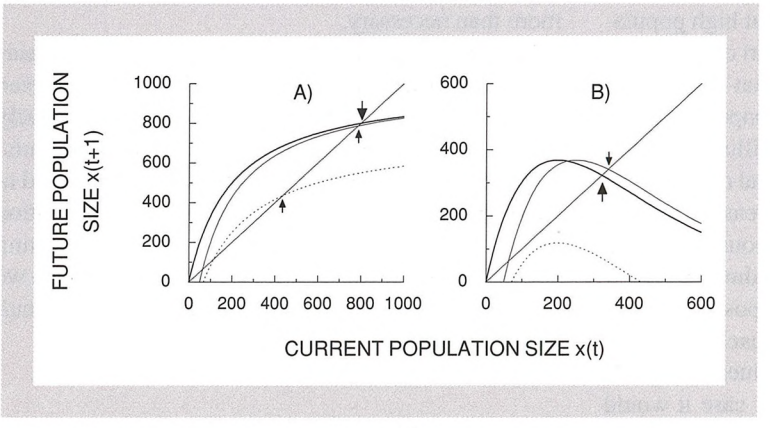


Figure 2. Post-breeding population sizes in populations subject to autumn or spring harvesting according to A) Beverton-Holt dynamics given by $f(x) = (1+\mu_0 x)^{-1}$, and B) Ricker dynamics, $f(x) = \exp(-\mu_0 x)$. Thick solid lines indicate unharvested dynamics, $x(t+1) = \lambda_0 x(t) f(x(t))$, where λ_0 indicates reproduction and $f(x(t))$ overwinter survival. Thin solid lines correspond to harvesting $k = 50$ individuals in the autumn, changing the dynamics to $x(t+1) = \lambda_0 (x(t)-k) f(x(t) - k)$, whereas dotted lines indicate harvesting $k = 50$ individuals in the spring, yielding $x(t+1) = \lambda_0 (x(t) f(x(t)) - k)$. Thus, autumn harvest shifts curves of density dependence to the right by k individuals, while spring harvest causes a downwards shift by $\lambda_0 k$. Equilibrium population sizes occur where the curves cross the diagonal $x(t) = x(t+1)$, marked with arrows (large arrows: unharvested population; small arrows: harvest in spring or autumn). Spring harvest has a much stronger detrimental effect on population growth than autumn harvesting. Also, spring harvesting cannot cause population size increases in the way that autumn harvesting can: in B) the harvested population has a higher equilibrium size than the unharvested population.

On the other hand, mistiming the harvest will be suboptimal regardless of the shape of density dependence. I have here considered two extremes only - harvesting immediately after or before the breeding season. More generally, it can be shown that the 'cost' of a harvest quota, in terms of a reduction of the breeding or post-breeding population size, becomes much larger as the season progresses even if the hunting does not specifically concentrate on the spring season

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(Kokko & Lindström 1998). This may be important especially for migrating populations such as many species of European waterfowl, for which hunting starts on the breeding grounds, continues during overwintering, and is for some species extended with a spring harvest season in the Baltic region (Lampio 1983).

Measuring compensatory and additive mortality

As shown in the previous section, a very essential part of estimating the effects of harvesting is to determine the degree to which hunting mortality is compensated (or even overcompensated) for by improved survival in the remaining individuals (Roseberry 1979). If removing part of the population does not improve the survival of the remaining individuals at all, hunting mortality is considered additive; otherwise, it is at least partly compensatory. Additive mortality means that sustainability can only be achieved if the population compensates by density-dependent reproduction. Complete compensation during the non-breeding season leads to unchanged population sizes at the beginning of the breeding season, and hence no density-dependent reproduction is needed for harvesting to be sustainable.

Theoretical considerations such as the above-mentioned can be used to examine various compensatory responses in hypothetical populations. However, the degree to which hunting is compensatory or additive in natural populations is much debated and probably varies among populations (e.g. Nichols, Conroy, Anderson & Burnham 1984, Ellison 1991, Dusek, Wood & Stewart 1992, Hellgren, Synatzske, Oldenburg & Guthery 1995). The usual approach to measure compensation (e.g. Burnham & Anderson 1984, Nichols 1991) is to estimate the slope b of the model

$$S_T = S_0 (1 - bK) \qquad (1),$$

where S_T denotes total survival (ratio of post-season and the initial population size), S_0 indicates natural survival, and K is the kill rate (interpreted as the ratio of hunting bag and initial population size, and estimated from band recovery rates). b = 1 suggests additive mortality, whereas b = 0 gives complete compensation. Sometimes, however, a different notation is used (e.g. Anderson & Burnham 1976), where b is defined by the equation $S_T = S_0 - (1\text{-}b)K$. With this formulation b = -1 indicates complete compensation, and additivity increases the value of b towards 0. I use here the more common convention of equation 1.

Equation 1 can be regarded as a 'black box' model of compensation, since it only relates the output (remaining population size) to the inputs (initial population size, and total bag removed), without considering any details in between. This is certainly advantageous as it probably remains a practical impossibility to estimate daily mortality rates and their dependence of current and previous population sizes in a way that would allow deriving the compensatory response from first principles. However, the message from theoretical work, viz. that the timing of the removal of individuals can have a profound effect on the population response, extends deeper than just proving that harvest timing is important. I will now show that it also means that the timing of hunting mortality influences the interpretation of measurements of additivity and compensation.

The 'black box' model of compensation is commonly interpreted in a way that assumes hunting mortality to precede all natural mortality. With an initial post-breeding population size x and a hunting bag of Kx individuals, the size of the population that enters the overwintering season is then (1-K)x. Of these individuals, the fraction S_0 survives if there is no compensation, such that the total survival becomes $S_0(1\text{-}K)$ (Equation 1 with b = 1). If there is complete compensation, the total survival S_T should equal S_0 despite a fraction (1-K) of individuals having been removed. This is possible if the survival of the remaining individuals is increased to $S_C = S_0/(1\text{-}K)$. S_T will, however, be bound to decrease after S_C has reached the unavoidable upper limit of 1 (survival of all the non-hunted individuals). These rules give the familiar shapes of additive and compensatory mortality (Fig. 3).

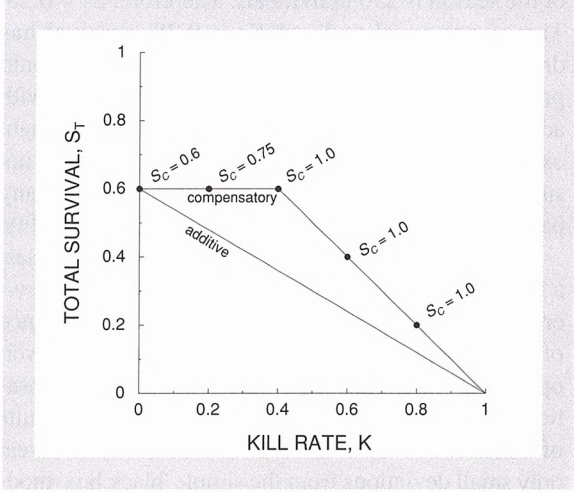


Figure 3. The 'black box' view of additive and compensatory mortality. Restoring $S_T / S_0 = 1$ after some hunting has occurred requires increasing the compensatory survival S_C. At $K \geq (S_0\text{-}1)/S_0$, the required S_C reaches the value 1, and further compensation is not possible (in this example, S_0 is set at 0.6).

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In practice, hunting very rarely occurs in a single stroke in time, and there are several reasons to suspect that a gradual removal of individuals will not have the same effect on the remaining population as their absence from the start of the season. At least, logic requires that the removal of an individual at time t cannot prevent natural deaths that occur prior to that date. An additional 'cost' of late harvesting exists if competition is caused by individuals depleting their food resources. In that case, it is unreasonable to assume that killing an individual late in the winter will improve the survival of others during the remaining time as much as if the killed individual had been absent from the start of the season. This is because it has, by the time of its death, already consumed some of the resources that would otherwise have remained available for others.

Furthermore, the timing of harvesting will affect the total survival rate even if hunting mortality does not influence natural mortality at all (the additive situation). This occurs simply because at a later point in the season, there will be a smaller population left, and defining the kill rate as the ratio of the bag and the initial population size will underestimate the true kill rate at any later time point. As a very simple example, we may consider an additive case with $S_0 = 0.4$, $K = 0.3$, and hunting taking place when 80% of the initially present population is still alive. With an initial population size of 1,000 individuals, $K = 0.3$ means removing 300 individuals but not out of 1,000, but of 800. At this stage, 500 individuals remain in the population. Assuming additivity, the natural survival after hunting is 0.5 (since $0.8 \times 0.5 = 0.4 = S_0$), and the population size at the end of the season is 250 individuals. Therefore, $S_T = 0.25$. This is not equal to S_0 (1-K) = 0.28; survival has dropped more than the discrete additive model would predict, and the correct value of b in Equation 1 with additive hunting mortality will be 1.25. A similar thought experiment shows that the compensatory model will not suffice to yield complete compensation whenever any part of the hunting occurs after some natural mortality.

Therefore, in both additive and compensatory cases, a later hunting season increases the value of b as fewer individuals are expected to survive. The importance of this problem was fully recognised in the original development of the estimation of additivity and compensation (Anderson & Burnham 1976), but here, the results of a detailed continuous-time model seemed to reveal only small deviations from the simple 'black box' model. However, as I shall show, these deviations can sometimes grow large.

Interpreting compensation graphs: a numerical example

In order to assess the magnitude of the deviations in b when hunting seasons vary in length, I give numerical results for three scenarios where the total bag is divided into daily harvesting during a non-breeding season ('winter' for short) that lasts 300 days. During these days, mortality occurs daily at a constant rate so that total survival equals S_0. Thus, daily survival s is solved from $s^{300} = S_0$. I study five time distributions of hunting: 1) immediately after breeding (t = 0); 2) in the first half of the winter season ($0 \leq t < 150$); 3) throughout the winter ($0 \leq t < 300$); 4) in the latter half of the winter season ($150 \leq t < 300$); 5) at the end of the winter, immediately before breeding (t = 300). Furthermore, in each case, hunting may either remove a constant number of individuals/day, or hunting effort may be kept constant such that the daily removal rate of individuals decreases as the population size decreases. The total kill rate K is simply summed as the ratio of the total bag that a given effort collects during the whole of the hunting season, and the initial population size, x, at the start of the winter.

These various timing choices of hunting can then be applied to three different scenarios of compensation. In the first, additive scenario, daily survival is assumed to be completely unaffected by the removal of individuals (Fig. 4: additive mortality). The second scenario (see Fig. 4: compensation I) assumes complete compensation, such that immediately after Kx individuals have been removed, the daily survival s(t) increases to a level defined by $s(t)^{300} = S_0/(1\text{-}K)$, though naturally not to levels higher than 100%. This level, were it applied over the whole season, would leave the number of survived individuals unaffected by hunting. The third case (see Fig. 4: compensation II) again assumes complete compensation if competitors are removed at an early stage, but effects of resource depletion are additionally considered. This is done by assuming that individuals remove resources at a constant rate while they are alive, and the death of one individual on day d therefore corresponds, from this day onwards, to the effect of having removed (300-d)/300 individuals at time t = 0. Expressed mathematically, this means that daily survival fulfils $s(t)^{300} = S_0/(1\text{-}K')$, where

$$K' = \sum_{i=1}^{k} \frac{300\text{-}d_i}{300}$$

sums the resources spared by the k individuals that have been killed through hunting by the time t, and the d_i denotes the timing of their deaths.

In all three cases, the 'black box' pattern of additive

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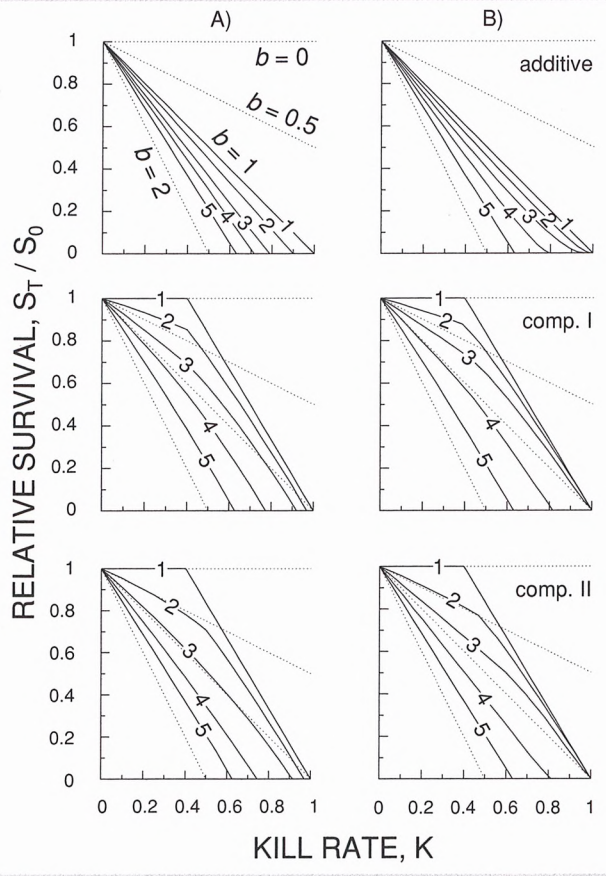


Figure 4. Additive and compensatory mortality when hunting extends over different periods of time in the overwintering season for A): a fixed quota resulting in kill rate K being obtained by removing an equal daily number of individuals during the hunting season, and B): the kill rate calculated from a fixed hunting effort during the season, such that daily kills are proportional to the remaining population. Solid lines give the predicted relationship between kill rate K and total survival S_T for five different scenarios: 1) All hunting occurs prior to natural mortality, 2) Hunting occurs in the first half of the winter season, 3) Hunting occurs throughout the winter, 4) Hunting occurs in the latter half of the winter season, and 5) All hunting occurs after natural mortality. Broken lines indicate slopes b = 0 (horizontal line), 0.5, 1 (diagonal), and 2, as indicated in the top left panel. All examples are derived using S_0 = 0.6. See text for details regarding the additive and the two compensatory scenarios.

or fully compensatory mortality arises if all hunting occurs prior to the start of natural mortality (timing alternative 1 in Figure 4). In this timing option, additive mortality follows the slope b = -1, and compensatory mortality has b = 0 up to a point after which it declines steeply. However, the slopes b instantly deviate from these values and become considerably steeper when the hunting season extends to overlap with some of the natural mortality (timing alternatives 2-5 in Figure 4). In fact, a population with completely compensatory ability will produce mortality curves much resembling the additive curve of the 'black box' model, or even producing values of b exceeding that of the characteristic value of additivity, b = 1. Truly additive mortality, on the other hand, does not always produce b = 1 either, but has it rather as a minimum value. Harvesting and natural mortality may therefore interact to produce relationships between kill rate and survival that appear 'superadditive'. Finally, if hunting occurs too late in the season, distinguishing between the three scenarios becomes impossible (see Fig. 4, timing choice 5). This simply means that one should not expect mortality compensation to operate when it has no time to do so, i.e. in the context of spring hunting. Whether the quota is fixed beforehand or results from a constant effort harvesting policy has very little impact on any of these results (see Fig. 4A-B).

What does compensation mean?

Do these results destroy the concepts of additivity and compensation? One possible viewpoint is that a manager is not necessarily interested in the precise mechanism of compensation or the lack thereof, but rather in the simple overall relationship between kill rate and survival. Hence, we should only call mortality completely compensatory or additive when the slope of b equals 1 or 0, regardless of the mechanism within the 'black box' (i.e. season) that produces the observed relation between final and initial population size. This viewpoint has the advantage that it restores the 'black box' model together with its estimation procedures (Burnham & Anderson 1984). Under this view, the present results then simply mean that (i) completely compensatory mortality operates under fairly restrictive conditions only, and where it is found, it indicates that natural mortality is confined to a later season than hunting mortality, and (ii) that the possibility of 'superadditive' mortality should be acknowledged.

Interestingly, estimated mortality rates can be found to be largely compensatory at least for some species, e.g. the red grouse *Lagopus lagopus scoticus* (Ellison 1991) and several species of waterfowl (Nichols et al. 1984, Nichols 1991; but see Conroy & Eberhardt 1983,

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Barker, Hines & Nichols 1991 and Rexstad 1992 for less compensatory responses). This suggests that hunting and natural mortality indeed do occur at different, non-overlapping times in these species. This fits nicely with the observed timing of natural mortality found in the red grouse (Hudson, Newborn & Robertson 1997) and waterfowl (Stout & Cornwell 1976, Kalchreuter 1990), showing a peak in late winter or early spring; however, Blohm, Reynolds, Bladen, Nichols, Hines, Pollock & Eberhardt (1987) report high fall-winter mortality in male mallards *Anas platyrhynchos*. Timing of hunting and natural mortality have also been shown to be separated in muskrats *Odantra zibethicus* and raccoons *Procyon lotor* (Clark 1990b, Hasbrouck, Clark & Andrews 1992). I know of no study where both compensation and timing of natural mortality were studied simultaneously in the same population. Rexstad (1992) shows that Canada geese *Branta canadensis* respond only weakly to variation in the length of the hunting season, which is attributed to the high survival rate of this species: removing one individual early or late will not cause a large difference in the number of natural deaths if this number is low in any case.

In any case, if such an operational definition of compensation is accepted, one should be aware of three complications. First, asking whether the 'black box' produces a compensatory response is not the same question as asking whether the survival of remaining individuals is improved by reduced population sizes. Consequently, an estimated slope near the value of total additivity, $b = 1$, cannot be used to infer that survival is density independent during the winter season, or that there is no intraspecific competition for resources. Even complete compensation at the individual level can produce such estimates via the 'black box' model if timing of harvest is ignored - and partial compensation is even more likely to do so. Second, if b is estimated by plotting observed survival against kill rates of various years, data points will be biased downwards in years when there has been overlap between the timing of natural and hunting mortality. Therefore, annual variation in timing of either of these sources of mortality will have a confounding effect on the estimation of b. Third, hunting regulations often operate through changing the length of the open season. Because of seasonality effects, the population size may respond much more drastically to an extended season than the mere increase in kill rates would suggest, if the season reaches a point in time where natural overwinter mortality becomes significant. Previous estimates of b cannot therefore be used as a basis for predicting population responses to changing harvest plans, if the changes include timing of the harvest season.

Conclusions

Because of density dependence, hunting strategies generally reflect a trade-off between two opposing preferences: a high yield and the maintenance of high population density. However, this is to a large extent an oversimplistic view: ignoring the details of the mating system, age structure, density dependence and seasonal behaviour of a population will easily cause hunting to be harmful to an unnecessary extent. This is especially evident in seasonally reproducing populations, where a simple mistiming of harvesting may cause drastic declines in the population, without improving the yield. On the other hand, detailed knowledge of density dependence could, in principle, be used to overcome the trade-off so that exploitation could increase the size of the breeding population. Even though such extreme cases occur only with specific forms of compensation, the conclusion that it pays to know more applies more generally; if individuals in populations differ from each other in any biologically significant way, a random cull is bound to be inferior to a more carefully planned harvesting strategy. Finally, theoretical models that predict population-level responses to harvesting based on basic compensatory processes deserve attention not only because they shed light on the underlying principles which sustainable harvesting has to rely on. They also warn against careless interpretation of empirical data, including extrapolation of previous results on compensation to new harvesting regulations.

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