Lecture 7. Additive vs. compensatory mortality and MSY.

Reading:

> Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory Mortality in waterfowl populations: a review of the evidence and implications for research and management. Transactions of North American Wildlife and Natural Resources Conference 49:535-554.

Optional:

> Nichols, J. D. 1991. Responses of North American duck populations to exploitation. Pages 498-525 *in* C. M. Perrins, J-D. Lebreton, and G. J. M. Hirons, eds. Bird Population Studies, Oxford, New York, New York, USA.
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> Smith, G. and R. Reynolds. 1992. Hunting and mallard survival. Journal of Wildlife Management 56:306-316.
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> Sedinger, J. S., and E. A. Rexstad. 1994. Do restrictive harvest regulations result in higher survival rates in mallards? A comment. Journal of Wildlife Management 58:571-577.
>
> Smith, G. and R. Reynolds. 1994. Hunting and mallard survival: a reply. Journal of Wildlife Management 58:578-581.
>
> Clark, W. R. 1987. Effect of harvest on annual survival of muskrats. Journal of Wildlife Management 51:265-272.

I will illustrate the concept of compensatory mortality with a simple example. Assume that 90 animals start the biological year. All harvest takes place before any natural mortality occurs, following the assumptions of Boyce et al. (1999). Further assume that the natural mortality occurs in density-dependent fashion, i.e., survival from the end of the harvest period to the start of the next year is defined as

$$S_n = \beta_0 - \beta_1 N \quad ,$$

where S_n is the survival from the end of the harvest period to the start of the next year, and let $\beta_0 = 0.8333$ and $\beta_1 = 0.0055556$. This function is plotted on the following graph, along with the density-independent situation where no response in survival is allowed as a function of population size. These lines are labels compensatory for density dependence and additive for density independence because these are the underlying assumptions that result in compensatory and additive mortality.

Survival vs. Population Size
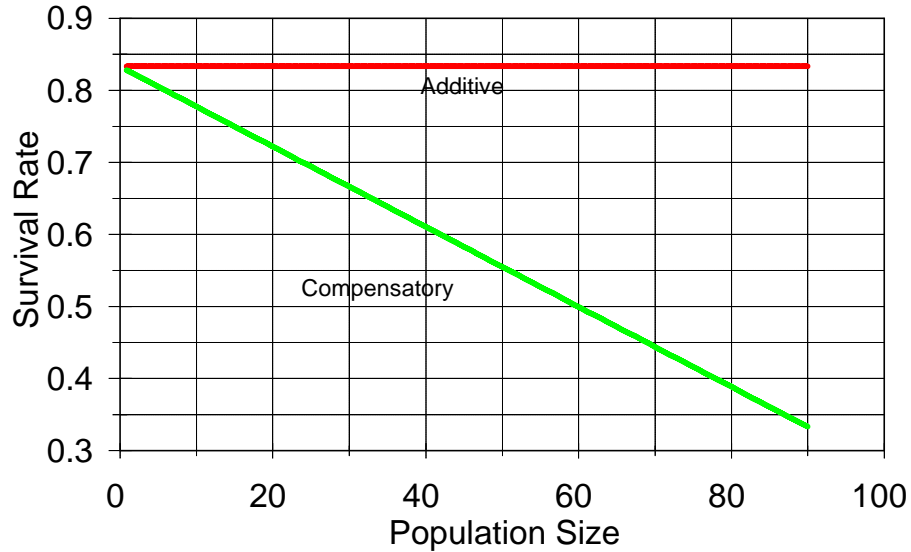
Assume now, that for the base situation, 1/3 of the 90 animals be removed by hunting, so that for the 60 left, $S_n = 0.8333 - 0.0055556(60) = 0.5$ under the assumption of density dependence. Thus, 30 of these animals survive the year.
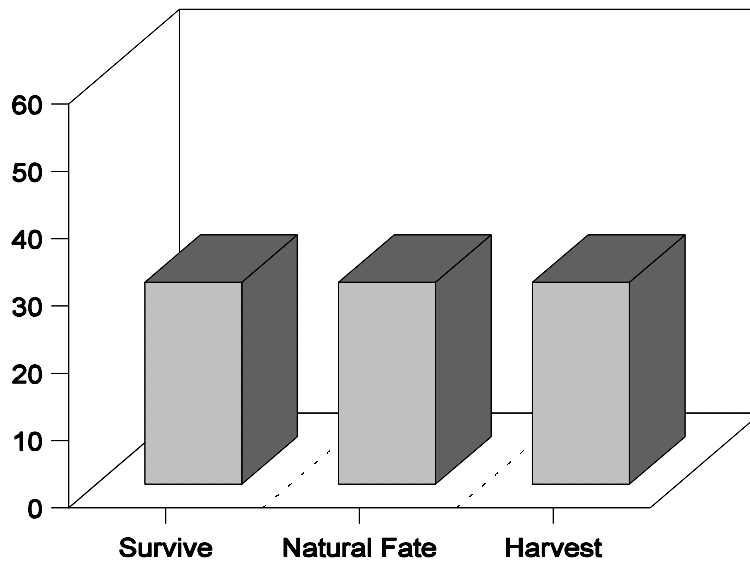
Now, we want to manipulate the system by removing the hunting mortality, i.e., let the harvest rate equal zero. Under the assumption of a density-dependent response to the

removal of hunting, 90 animals undergo natural mortality, and the survival rate is S_n = 0.8333 - 0.0055556(90) = 0.3333. Thus, only 30 animals survive the year, just as in the case of hunting mortality of 33%.
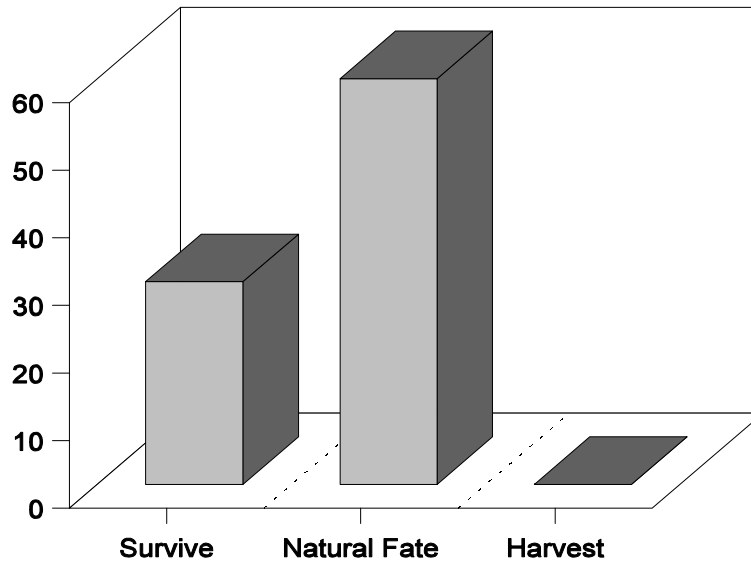

The hunting mortality is compensated for by an increase in survival of the animals remaining after the hunting season by the density-dependent decrease in mortality because of fewer animals present in the population. The overall survival rate for the year (S, with no subscript) is defined as a function of the harvest rate (h) and the survival rate after the hunting season. The overall survival rate will be the product of the survival through the hunting season (1 - h) and S_n. For the case where mortality is density-dependent (i.e., S_n is a function of density):

$$S = (1 - h)[\beta_0 - \beta_1(N - hN)] \quad .$$

If we graph the overall survival rate (S), we get the relationship:

Harvest Rate vs. Annual Survival Rate
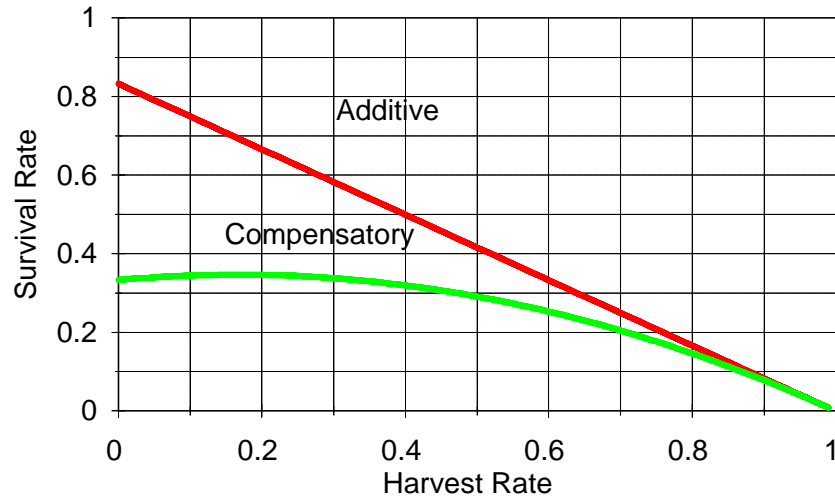
This curve of compensation is relatively flat for quite a range of harvest rates, because the natural survival rate compensates for the increase in harvest rate by increasing because of the decreasing number of animals in the population. The maximum overall survival is obtained at

$$h = \frac{2N\beta_1 - \beta_0}{2N\beta_1} \quad .$$

For the values of $\beta_0 = 0.8333$, $\beta_1 = 0.005556$, and $N = 90$, the maximum survival is obtained at a harvest rate of $h = 0.16667$.

If the hunting mortality had been additive, then the survival rate after hunting observed for the 60 animals in the base situation would continue to apply to 90 animals, so that 45 would survive the year. This situation is demonstrated in the following histogram, and is illustrated in the above plot by the line labeled additive. No response in the natural mortality rate is available to compensate for increased harvest, so the additive line decreases linearly in response to an increase in the harvest rate.
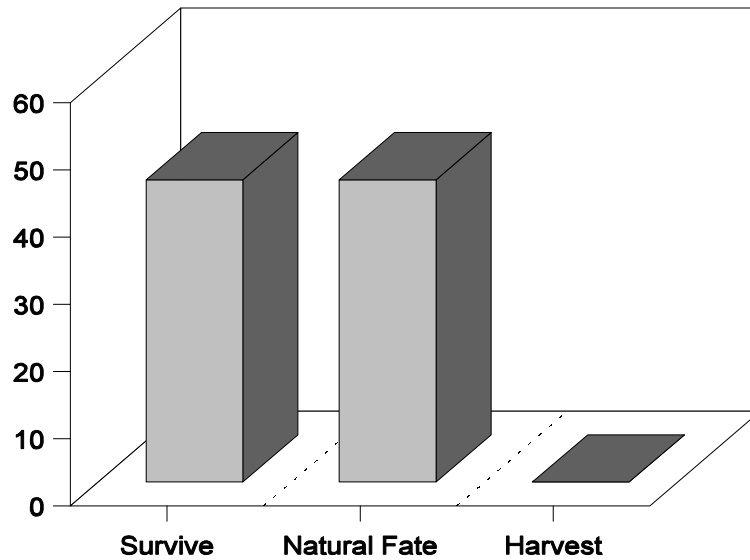
Another common misconception about our example is that if the harvest is removed, all the harvested animals will live, giving the following result. This result I label super additive. To achieve this response in a population, you would have to have reverse density-dependence, i.e., the natural mortality rate would have to decrease as the population increased.
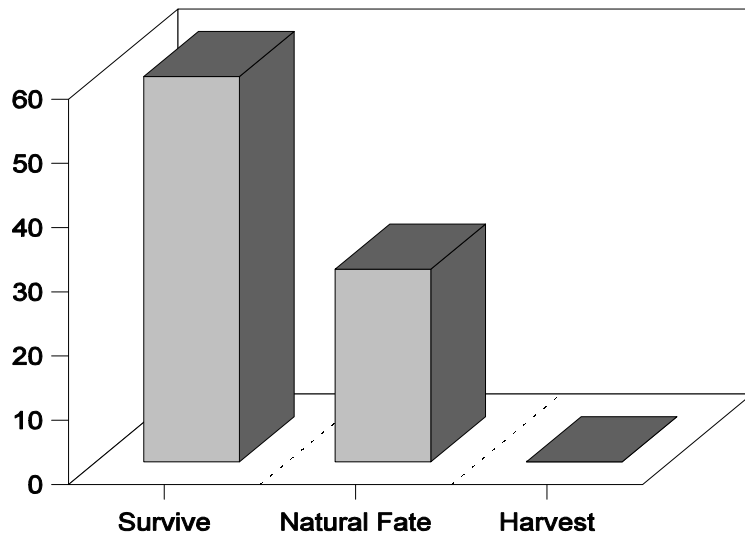

Anderson and Burnham (1976) presented a mathematical argument for compensatory mortality. They derived their results based on instantaneous rates of harvest and natural mortality. The example above is based on finite rates, with the assumption of no natural mortality during the harvest period. For finite rates and no natural

mortality during the hunting season, their additive mortality results are the same straight line graph as shown above. However, if some natural mortality occurs during the hunting season, the line deviates below the straight line shown above.
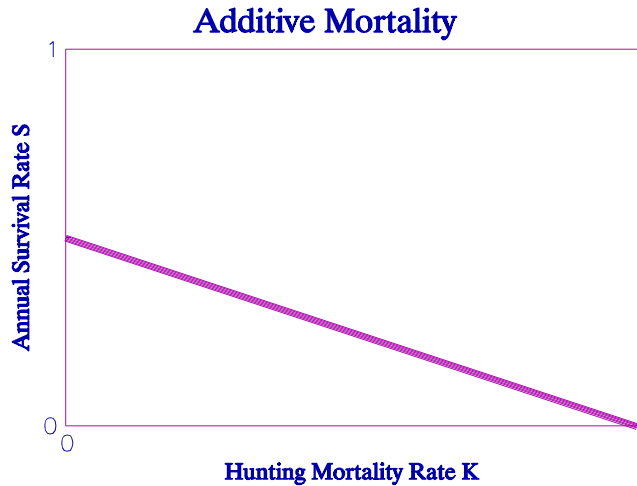

Under the compensatory mortality hypothesis with density dependence operating on survival rate after the hunting season, Anderson and Burnham (1976) present the following graph. The shape and general conclusions reached from this graph are the same as illustrated above. Over some range of harvest (0 to c), the annual survival rate remains unchanged in response to harvest. However, beyond the threshold value of harvest (c), the density-dependent response of the population cannot compensate for the harvest, so the annual survival rate declines.
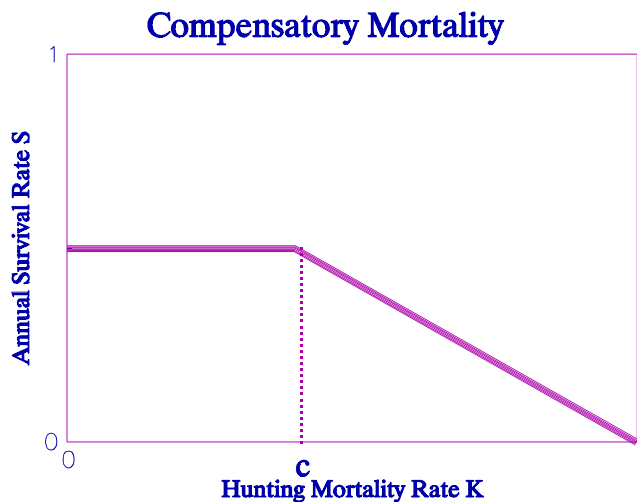
The natural mortality function to generate such a survival function in response to hunting mortality is the following. The population identified with c corresponds to the population size at the threshold in the above graph. The x-axis is the post-hunt population size, and the y-axis is the mortality rate from post-harvest to the start of the next year. Any

population harvested at a rate greater then c has no natural mortality following harvest, thus illustrating complete compensation.

Natural Mortality vs. Population Size
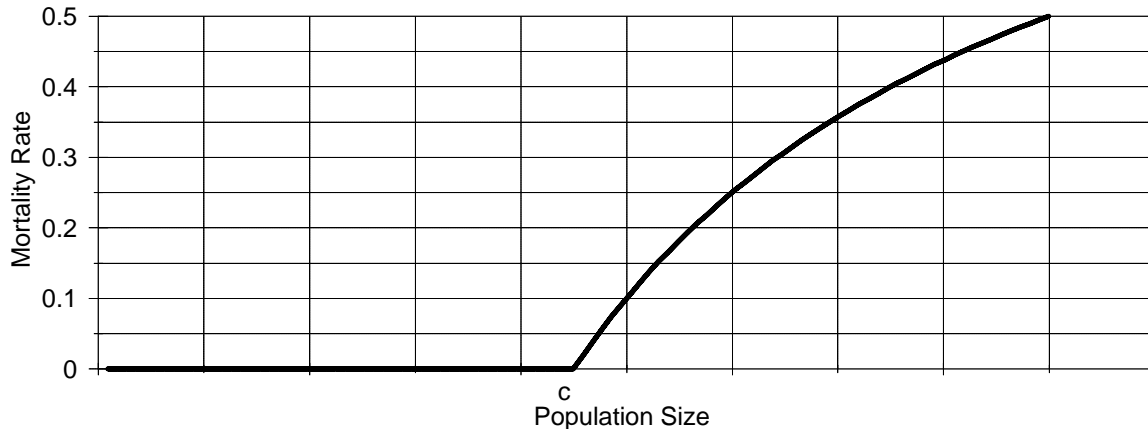
Three approaches have been used to test between the 2 hypotheses

Regression of $\hat{S}_i$ vs. $\hat{K}_i$, where K is kill rate, not carrying capacity. Sampling covariance of the 2 estimates $\hat{S}_i$ and $\hat{K}_i$ induces a negative relationship (Burnham and Anderson 1979). This covariance must be removed to compute a proper test of these 2 quantities.

Splitting raw data in half (Nichols and Hines 1983) is one approach to removing the covariance. Half the data are used to estimate $\hat{S}_i$ and the other half to estimate $\hat{K}_i$.

Both hypotheses in a single equation (Burnham et al. 1984)

$S_i = S_0(1 - bK_i)$
H_0: $b = 0$ means compensation
H_a: $0 < b < 1$ means partial compensation
H_a: $b = 1$ means additive

Continuity of compensatory and additive hypotheses

Relation of survival to population size (or harvest)

Instantaneous vs. finite representations

$N_t = N_0\exp\{[b - (m_0 + n_0 - m_0n_0)]t\}$ where m_0 is fishing mortality in the absence of natural mortality, and n_0 is natural mortality in the absence of fishing mortality. This equation assumes additive mortality. The term m_0n_0 just specifies that a fish cannot die from both natural and fishing mortality. In reality, m_0 can never be measured (see Anderson and Burnham 1981). The parameters m and n are actually measured, so that overall mortality is $m + n$ which conceptually is not equal to

$m_0 + n_0 - m_0n_0$.

For compensatory mortality, n must be made a function of m.

Another example for the finite time model of how compensation can be significant assumes that density-dependent mortality (m), i.e., the mortality rate for the period post-harvest until the start of the next year, is modeled by the following function:

$$m = \exp(\beta_0 + \beta_1(N - hN)^\theta) ,$$

or equivalently, survival as a function of density,

$$S_n = 1 - \exp(\beta_0 + \beta_1(N - hN)^\theta) .$$

Plug the values $\beta_0 = 1.79175$, $\beta_1 = 2.2\text{E-8}$, and $\theta = 4$ into this function. The resulting curve as a function of N with $h = 0$ looks like this.
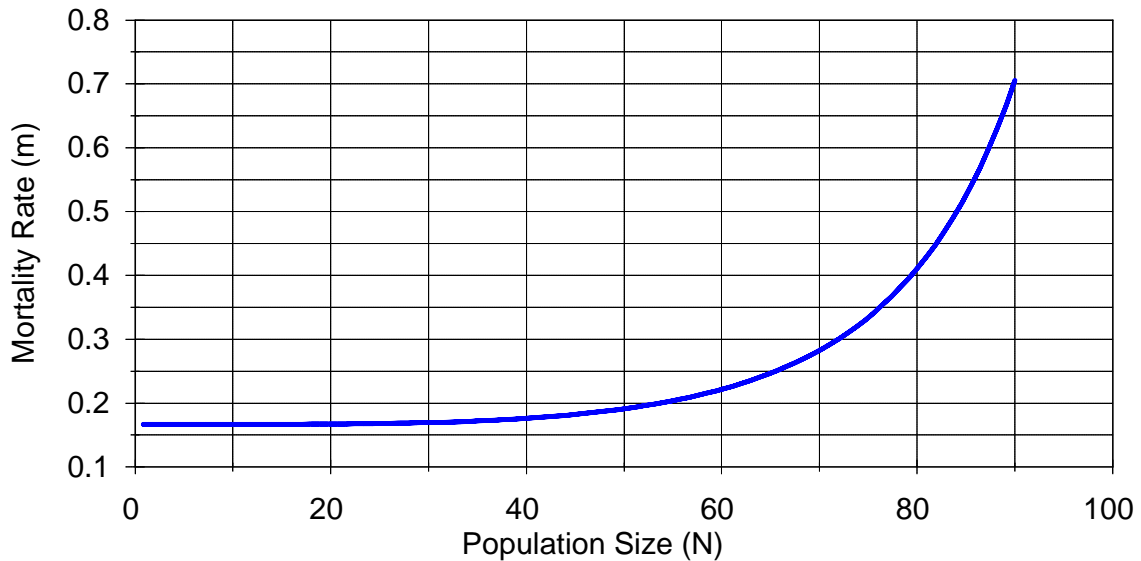
 Plugging this density-dependent mortality curve into the expression for overall survival, i.e., the product of survival through the harvest period and the survival through the period from the end of harvest until the start of the next year (S_n) gives

$$S = (1 - h)\{1 - \exp[\beta_0 + \beta_1(N - hN)^\theta]\} ,$$

and results in a curve of survival rate as a function of harvest rate like the following.
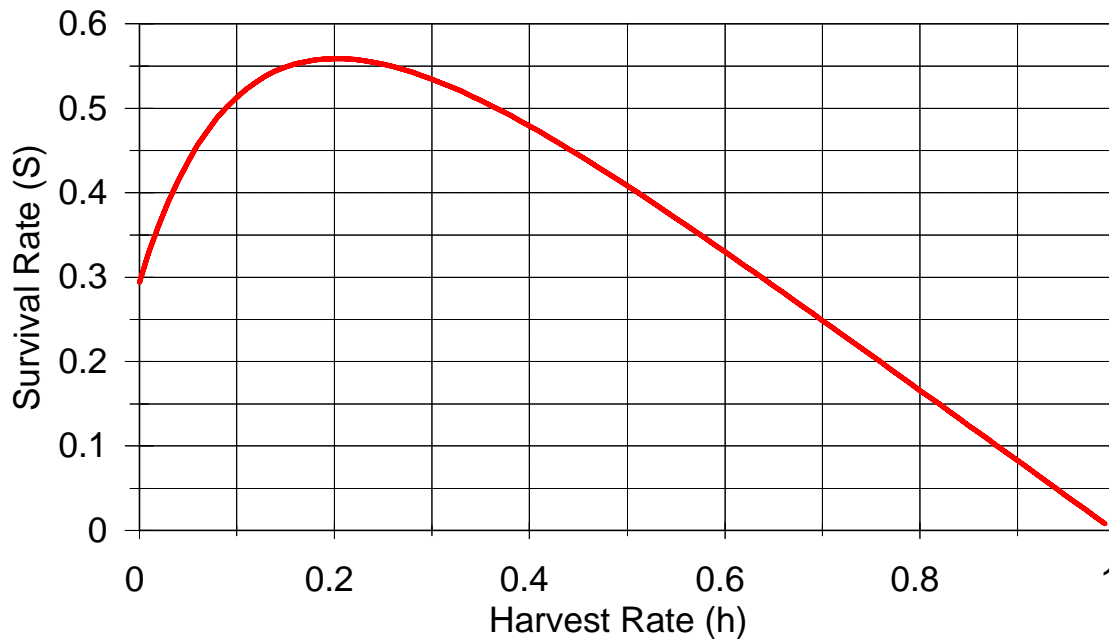
In other words, as one of my game warden friends says, "you gotta shoot'm to save'm". A harvest rate of about 0.2 results in the maximum number of animals at the end of the winter, far more than if harvest is zero. With this mortality function, you can harvest up to just more than 60% of the population, and still have the same number of animals left at the end of the year as you would have with no harvest.

Examples.
> Waterfowl (Burnham and Anderson 1984, Burnham et al. 1984, Nichols et al. 1984, Smith and Reynolds 1992, Sedinger and Rexstad 1994, Smith and Reynolds 1994)
> Muskrats (Clark 1987)
> Mule deer (Bartmann 1992)

Discussion.
> Why have so many studies examined reproduction in response to population size, but not survival rates?

Literature Cited

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Sedinger, J. S., and E. A. Rexstad. 1994. Do restrictive harvest regulations result in higher survival rates in mallards? A comment. Journal of Wildlife Management 58:571-577.

Smith, G. and R. Reynolds. 1992. Hunting and mallard survival. Journal of Wildlife Management 56:306-316.

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