

Assessing the impact of spring hunting on waterfowl populations

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Received 24 August 1998, accepted 13 October 1998

Harvesting prior to the breeding season is widely considered ‘unwise’ since it has the bearing of deducting from the capital. However, spring hunting is still a common practice in many parts of the world, and its true effects remain uninvestigated. We present a model to investigate the range of possible effects of spring harvesting on waterfowl populations. The cost of spring harvesting is defined as corresponding loss in harvest opportunities in autumn; this cost may be sex-specific. Factors increasing the cost are monogamy, high breeding output, high summer survival and weak density dependence in summer, such that the population is mainly regulated through winter conditions. If the relative success of unpaired individuals is high (as in polygynous species if males are abundantly available after spring hunting), the cost of killing females may increase while that of killing males is reduced. Spring sex ratios may be more important in determining the cost than whether hunting occurs before or after pairing. Killing males can have surprisingly high costs and they may even exceed the cost of killing females if sex ratios are female-biased.

1. Introduction

Regulation of the length and timing of the hunting season are key factors in the management of the harvest for sustaining migratory waterfowl populations. The timing of the closing date is of primary importance because it may be unwise to harvest populations in late winter and spring when natural mortality has already taken its effect (Kok-

ko & Lindström 1998). In addition, because pairing in many species begins already in late autumn (Bluhm 1988), hunting after midwinter may seriously affect pair formation and reproduction. However, late-winter or spring harvesting is still a common practice in many parts of the world. For example, open season for duck shooting in many European countries extends to February–March, and in some countries limited hunting is

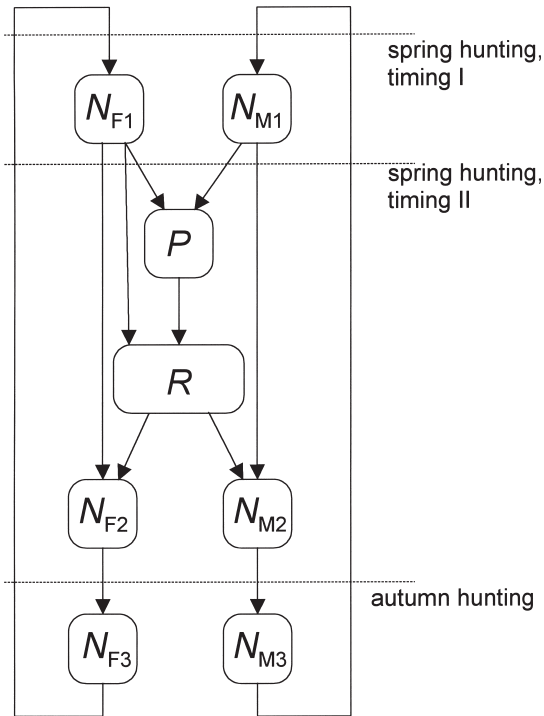


Fig. 1. A flow diagram of the seasonal model. It is assumed that the goal is to maintain a stable population despite hunting, such that each population size N remains constant. Pair formation P is affected by the spring population sizes N_{F1} (females) and N_{M1} (males) only if hunting occurs early enough (timing I), but hunting will affect pair formation directly if timing II is used. The number of pairs P creates breeding output R but not alone: the total number of females that survive the spring hunting period also contribute to P directly since unpaired females may have some breeding success. The post-breeding population sizes N_{F2} and N_{M2} are subject to autumn hunting, and a fraction of the remaining individuals, N_{F3} and N_{M3} , survives over winter and forms the new N_{F1} and N_{M1} .

allowed even in April and May (Lampio 1983, information from the 1980–81 hunting season). A recent inquiry into the harvesting of the migratory birds of the Western Palearctic flyway reveals that closing dates in Europe and in some North African countries have not changed during the last 15 years (Migratory Birds of the Western Palearctic; R. Pouget, pers. comm.). In Russia and North America, ‘subsistence’ spring hunting is allowed with a considerable number of birds shot each year (Kostin 1996, Thompson 1996). Yet another recent example comes from North-East

China where hunting is allowed from early April to mid-May, a period immediately preceding the local breeding season (Li 1996).

Considering the apparent contradiction between spring hunting and the premise of sustainable use of waterfowl it is surprising that consequences of spring hunting for waterfowl populations have remained virtually uninvestigated. The only empirical work we are aware of is that by Hario *et al.* (1995) on the common eider (*Somateria mollissima* L.) in Finland. They found that experimental removal of males by spring shooting caused a significant decrease in the hatching success in nests of widowed females. Hario *et al.* (1995) concluded that the effect of spring shooting on the reproduction of eiders acted via reduced remating potential. Clearly, there is a need for further research on the topic. In this paper, we take a modelling approach to investigate the range of possible effects of spring harvesting on waterfowl populations.

When aiming at a quantitative analysis, it is desirable to seek a currency of the effects of harvesting to enable comparing different timing decisions. A decrease in equilibrium population size is usually expected in harvested populations (Robertson & Rosenberg 1988), but defining this as the ‘cost’ of harvesting implies difficulties as hunting in different times will affect equilibrium sizes differently depending on when they are measured (H. Kokko, unpubl.). Furthermore, the relationship between population size and persistence or conservational value is unlikely to be linear. Instead, we have defined the cost of spring harvest very pragmatically in terms of harvest loss at the other possible option, autumn harvest of the same year. Here, the cost of spring hunting is expressed as the number of surplus individuals that could have been added to the autumn bag, if the spring individual had not been killed.

An alternative way to express this is that if counterbalancing the loss of one individual in the spring harvest requires refraining from killing C individuals in the autumn, the cost of spring harvest equals C . The spring and autumn harvests are, thus, balanced in this choice model so that both give equal population sizes after the autumn season, and overwinter survival is not affected. Note that the cost is expressed in terms of an increase or decrease of the current autumn hunting

bag rather than by a comparison to a hypothetical, non-harvested population; we believe that our choice is the more realistic one when considering gamebirds.

2. The model

We aim at finding the range of possible population-wide responses to spring harvest by a seasonal, sex-specific model that incorporates density dependence (Fig. 1). The population cannot be represented by a single equilibrium size since harvest has a different effect depending on the timing; also, males and females may experience different mortality at different times of a year (e.g., Blohm *et al.* 1987, Johnson *et al.* 1992). Considering males and females separately is essential, as spring hunting may be confined to males only in some species but not in others: e.g., in Finland, spring hunting affects male eiders *Somateria mollissima*, goldeneyes *Bucephala clangula*, red-breasted mergansers *Mergus serrator* and goosanders *Mergus merganser*, but both male and female long-tailed ducks *Clangula hyemalis* (T. Veistola, pers. comm.). Moreover, if breeding success and survival are density-dependent, the most relevant figure might not be the total population density but the density of either males or females, e.g., if males and females do not share the same habitat during the breeding season. Hence, we identify the following eight different population sizes:

N_{F1}, N_{M1}	Spring population, females and males,
P	Number of breeding pairs in spring,
R	Number of recruits (fledged young) after summer,
N_{F2}, N_{M2}	Autumn population before hunting, females and males, and
N_{F3}, N_{M3}	Autumn population after hunting, females and males.

Additionally, we assume the following:

1. The sex that is in short supply in the spring will determine the number of pairs, P . However, some unpaired individuals may remain even in this sex. We denote the fraction of paired individuals of the minority sex by α ($0 < \alpha \leq 1$). Thus, if females are the minority sex, we have (without spring hunting) $P =$

αN_{F1} ; otherwise $P = \alpha N_{M1}$. To simplify the notation, we denote the minority sex by \Downarrow and the majority sex by \Uparrow , which gives $P = \alpha N_{\Downarrow 1}$ in either case.

2. The breeding success of an unpaired female is not necessarily 0, but a fraction β of the success of a paired female ($0 \leq \beta \leq 1$). β will be high if the male does not provide much parental care, and at least one of the following conditions is met: (i) remating is possible for a female who loses her mate in spring hunting, (ii) insemination has already taken place before spring hunting, or (iii) extra-pair fertilisations are common.
3. At each stage, density dependence may act within a single sex, indiscriminately among both sexes, or in any intermediate combination. This is accomplished by varying the slopes of survival and breeding success against male or female population size independently. If the slopes are equal, density dependence is indiscriminate. Some stages may lack density dependence (slope = 0).
4. Sex ratio of recruits can be approximated by 1:1.
5. Current practice is to hunt H_{F1} females and H_{M1} males in the spring, and H_{F2} females and H_{M2} males in the autumn. If the aim is to investigate effects of opening a yet non-existing spring harvest season, we set $H_{F1} = H_{M1} = 0$.
6. Spring hunting may occur either before (timing I, Fig. 1) or after (timing II) pairs have been formed; these two extremes should give the possible range of outcomes.

Timing of spring hunting will obviously affect pair formation. In timing I, we simply have $P = \alpha N_{\Downarrow 1}$. In timing II, the relationship is more complicated. The hunting of one individual of the minority sex will decrease P by α (the probability that the individual was paired). The probability of being paired in the majority sex is $\alpha N_{\Downarrow 1} / N_{\Uparrow 1}$. The fraction $N_{\Downarrow 1} / N_{\Uparrow 1} < 1$ by definition as $N_{\Downarrow 1}$ is the minority sex. The number of pairs is therefore affected less if the sex that is available in surplus is hunted. Note that we assume that culling males and females reduces P independently. This is not strictly true if hunting often kills both individuals from a pair, but it is a good approximation if spring hunting is either a reasonably rare cause of mortality or strongly biased towards one sex.

Because of density dependence, breeding and survival parameters are functions of female and male density, e.g., overwinter mortality of males depends on both male and female numbers at the start of winter. To keep a close touch to reality, the recruitment and survival parameters are incorporated in the model at the relevant hunting pressure that is currently in use; that is, e.g., overwinter survival of females, W_F , is measured at population sizes N_{F3} and N_{M3} when timing II is used.

The equations that determine the equilibrium size depend on whether timing I or II is used. To achieve an equilibrium, a chain of the following equations has to be fulfilled so that the loop closes in Fig. 1:

1. Pair formation:

timing I:
$$P = \alpha N_{\downarrow 1} \quad (1)$$

timing II:
$$P = \alpha N_{\downarrow 1} - \alpha H_{\downarrow 1} - \alpha \frac{N_{\downarrow 1}}{N_{\uparrow 1}} H_{\uparrow 1}$$

2. Breeding with average success B per paired female, and βB per unpaired female. B is a function of both female and male numbers.

timing I:
$$R = (P + \beta(N_{F1} - P)) \times B(N_{F1}, N_{M1}) \quad (2)$$

timing II:
$$R = (P + \beta(N_{F1} - H_{F1} - P)) \times B(N_{F1} - H_{F1}, N_{M1} - H_{M1})$$

3. Recruitment and summer survival of females and males. Survival S is a function of both female and male numbers.

timing I:
$$\begin{aligned} N_{F2} &= R/2 + N_{F1} \times S_F(N_{F1}, N_{M1}) \\ N_{M2} &= R/2 + N_{M1} \times S_M(N_{F1}, N_{M1}) \end{aligned} \quad (3)$$

timing II:
$$\begin{aligned} N_{F2} &= R/2 + (N_{F1} - H_{F1}) \\ &\quad \times S_F(N_{F1} - H_{F1}, N_{M1} - H_{M1}) \\ N_{M2} &= R/2 + (N_{M1} - H_{M1}) \\ &\quad \times S_M(N_{F1} - H_{F1}, N_{M1} - H_{M1}) \end{aligned}$$

4. Autumn hunting:

$$\begin{aligned} N_{F3} &= N_{F2} - H_{F2} \\ N_{M3} &= N_{M2} - H_{M2} \end{aligned} \quad (4)$$

5. Overwinter survival W and (in timing I) subsequent spring harvesting:

timing I:
$$\begin{aligned} N_{F1} &= N_{F3} \times W_F(N_{F3}, N_{M3}) - H_{F1} \\ N_{M1} &= N_{M3} \times W_M(N_{F3}, N_{M3}) - H_{M1} \end{aligned} \quad (5)$$

timing II:
$$\begin{aligned} N_{F1} &= N_{F3} \times W_F(N_{F3}, N_{M3}) \\ N_{M1} &= N_{M3} \times W_M(N_{F3}, N_{M3}) \end{aligned}$$

If the yearly bag and sex-specific population numbers are known both in spring and in autumn (either after or before hunting), most of the remaining parameters follow from these equations. As a hypothetical example, assume that the spring population (before hunting) equals 8 000 females and 10 000 males, the spring bag is confined to males such that 250 are shot, the autumn census (before hunting) gives 28 000 females (6 000 adults and 22 000 juveniles) and 30 000 males (8 000 adults and 22 000 juveniles), and the autumn bag equals 5 000 females and 5 000 males. Then, e.g., overwinter survival of males must equal 0.4, since 10 000 survived out of 25 000 that remained after the autumn hunting season, and summer survival of adult males equals 0.82. However, because of stochastic annual variation such equilibrium calculations may remain difficult in practise (e.g., Burnham *et al.* 1984), and it is usually also impossible to sex or age all individuals in the autumn census. Additionally, due to methodological problems and e.g. seasonal dispersal patterns, it is in practise very difficult to obtain comparable population estimates in spring and autumn.

Defining the cost of spring hunting in terms of autumn losses requires additionally knowledge of the density-dependent responses in B and the survival parameters S and W . Writing, e.g., $B'_M = -0.0001$ indicates that per female breeding success at the current population size, B decreases by 0.0001 if one male is added to the spring population. This slope may differ from the effect of adding a female, especially if summer habitat use differs among sexes. Similar expressions are used to denote density dependence in survival. Estimating these values is a daunting task. Our aim here is to provide an analytical result that shows the effect of each slope, which should be indicative of the different possibilities of spring costs. Considering the life history of a species, and the likely timing of the factors that limit its population, should then give some insight to the cost.

The cost of spring harvesting, C , will be sex-specific since females and males have a different role in producing the recruitment population in summer. We define C_F and C_M as the costs of hunting one female or male, respectively, in the spring.

The calculation of these costs is then straightforward: we determine how much adding one individual to the current spring bag (H_{F1} or H_{M1}) will decrease the total size of the autumn population, $N_{F2} + N_{M2}$.

3. Forms of the cost of spring harvesting

Eqs. 1–5 give us four possibilities for population equilibria: spring sex ratio may be male- or female-biased, and timing I or II may be used. For each possibility we will calculate C_F and C_M . Eqs. 1–5 determine how much adding one additional individual to the spring bags H_{F1} or H_{M1} will decrease $N_{F2} + N_{M2}$, so that the costs will equal the derivatives:

$$C_F = -\frac{d(N_{F2} + N_{M2})}{dH_{F1}}, \quad C_M = -\frac{d(N_{F2} + N_{M2})}{dH_{M1}} \quad (6)$$

once the relationship between the spring hunting bag and the autumn population size is known. This relationship is obtained by substituting P from

Eq. 1 for P Eq. 2, R from Eq. 2 for R Eq. 3, etc. Taking derivatives of this nested equation, we obtain results for the costs of harvesting in spring (Table 1).

All the costs in Table 1 have a common structure i.e., they are sums of five different effects, possibly scaled by a variable factor x , in the following way:

1. S_F or S_M — a cost derived from the fact that an individual killed in spring will not be present in the autumn. This cost trivially equals the survival probability of the individual over summer (S_F or S_M).
2. $x \times B$ — the direct loss of breeding output. This is a linearly increasing function of B , the per-capita breeding success of a paired female. The cost fraction x of B varies depending on the timing of shooting, and the sex of the killed individual, e.g. in timing I, and where the spring sex ratio is female-biased, the breeding cost of killing a male is $\alpha(1 - \beta)B$. Thus, the cost increases with the probability that the male was paired (α), and decreases if unpaired

Table 1. Costs of hunting one female (C_F) or one male (C_M) in spring, depending on harvest timing and spring sex ratios. See text for explanation of the symbols.

1. Timing I (before pair formation), female-biased spring sex ratio:

$$C_F = S_F + \beta B + N_{F1} \times (S_F)'_F + N_{M1} \times (S_M)'_F + (\beta N_{F1} + \alpha(1 - \beta)N_{M1})B'_F$$

$$C_M = S_M + \alpha(1 - \beta)B + N_{F1} \times (S_F)'_M + N_{M1} \times (S_M)'_M + (\beta N_{F1} + \alpha(1 - \beta)N_{M1})B'_M$$

2. Timing I, male-biased spring sex ratio:

$$C_F = S_F + (\beta + \alpha(1 - \beta))B + N_{F1} \times (S_F)'_F + N_{M1} \times (S_M)'_F + (\beta + \alpha(1 - \beta))N_{F1}B'_F$$

$$C_M = S_M + N_{F1} \times (S_F)'_M + N_{M1} \times (S_M)'_M + (\beta + \alpha(1 - \beta))N_{F1}B'_M$$

3. Timing II (after pair formation), female-biased spring sex ratio:

$$C_F = S_F + \left(\beta + \alpha(1 - \beta) \frac{N_{M1}}{N_{F2}} \right) B + (N_{F1} - H_{F1})(S_F)'_F + (N_{M1} - H_{M1})(S_M)'_F + \left(\beta(N_{F1} - H_{F1}) + \alpha(1 - \beta) \left(N_{M1} \left(1 - \frac{H_{F1}}{N_{F1}} \right) - H_{M1} \right) \right) B'_F$$

$$C_M = S_M + \alpha(1 - \beta)B + (N_{F1} - H_{F1})(S_F)'_M + (N_{M1} - H_{M1})(S_M)'_M + \left(\beta(N_{F1} - H_{F1}) + \alpha(1 - \beta) \left(N_{M1} \left(1 - \frac{H_{F1}}{N_{F1}} \right) - H_{M1} \right) \right) B'_M$$

4. Timing II, male-biased spring sex ratio:

$$C_F = S_F + \left(\beta + \alpha(1 - \beta) \left(1 - \frac{H_{M1}}{N_{M1}} \right) \right) B + (N_{F1} - H_{F1})(S_F)'_F + (N_{M1} - H_{M1})(S_M)'_F + \left(\beta(N_{F1} - H_{F1}) + \alpha(1 - \beta) \left(N_{F1} \left(1 - \frac{H_{M1}}{N_{M1}} \right) - H_{F1} \right) \right) B'_F$$

$$C_M = S_M + \alpha(1 - \beta) \left(\frac{N_{F1}}{N_{M1}} \times \frac{H_{M1}}{N_{M1}} \right) B + (N_{F1} - H_{F1})(S_F)'_M + (N_{M1} - H_{M1})(S_M)'_M + \left(\beta(N_{F1} - H_{F1}) + \alpha(1 - \beta) \left(N_{F1} \left(1 - \frac{H_{M1}}{N_{M1}} \right) - H_{F1} \right) \right) B'_M$$

females perform almost as well as paired ones (high β). A similar structure is found in the other alternatives as well. The only case where there is no direct breeding cost, is timing I where the spring sex ratio is male-biased. It is only logical that if pairing has not yet happened and males exist in surplus, spring hunting of males will not affect the number of paired or unpaired females as long as the male surplus is not completely exhausted.

3. $x \times (S_F)'$ — density dependence in the summer survival of females. This effect is present in all cases, and it equals the number of females present after spring hunting ($x = N_{F1}$ in timing I, and $x = N_{F1} - H_{F1}$ in timing II) multiplied by the density dependence in per-capita survival. The density dependence is measured against the number of females, $(S_F)'_F$, or the number of males, $(S_F)'_M$, depending on whether a female or a male is shot. These derivatives are negative if the per-capita survival of females decreases with an increasing number of females or males present; thus, they represent a decrease in the cost of spring hunting through compensatory survival. If males and females do not share a common habitat in summer, we will have $(S_F)'_M = 0$, and no compensation is possible. If, on the other hand, males and other females are equally severe competitors for a female in summer, we will have $(S_F)'_F = (S_F)'_M$.
4. $x \times (S_M)'$ — density dependence in the summer survival of males. This is analogous to the above cost, as it equals the number of males surviving the spring hunting season multiplied by $(S_M)'_F$ or $(S_M)'_M$, i.e. the density dependence of male survival against female or male numbers.
5. $x \times B'$ — compensatory density dependence in breeding output. This cost is negative if per-capita breeding success decreases with an increasing number of males ($B'_M < 0$) or females ($B'_F < 0$), i.e. it is a compensatory effect. The fraction x is complicated in most cases, but it always increases both with α and β (since if $0 < \beta < 1$, $0 < \alpha < 1$, and $x \geq y > 0$, the term $bx + \alpha(1 - \beta)y$ is an increasing function of both α and β).

It is notable that overwinter survival does not enter the cost equations. This happens merely be-

cause we defined the cost of spring harvesting in terms of the loss in the bag the following autumn that is necessary for compensating the spring reduction; thus, winter numbers will not be affected. However, the equations could equally well be rewritten by substituting winter survival values through the equilibrium relationships in Eqs. 1–5.

4. What do the cost functions imply?

Put in practical terms, how harmful is spring hunting in all the various cases? The true costs (factors that increase C) in Table 1 arise from S and B , summer survival and breeding output. Summer survival S is restricted to be ≤ 1 , whereas breeding output B can be high: as an example, the number of immature individuals in autumn often exceeds the sum over all other age classes in the mallard (Kaminski & Gluesing 1987). Clearly, this means that whenever $S + x \times B$ appears with a sufficiently large x in the equations, the cost of a killed spring individual may reduce the possible autumn bag by much more than one individual; this is the deduction from the breeding capital. A positive x is not confined to hunting females: male hunting incurs a high cost especially if spring sex ratio is female-biased, if pairs have already been formed before spring hunting (timing II), if most females have been paired (high α), and if an unpaired or widowed female has low breeding success (low β). A violation of one of these conditions reduces the cost of killing males, but the breeding cost decreases to 0 only if timing is strictly of type I, and spring sex ratio is female-biased, or if unpaired females suffer no reduction in their breeding success at all ($\beta = 1$). In these two cases, the absence cost S_M of males is the only true cost for male hunting — provided that persistent hunting of males does not turn the spring sex ratio towards female-biased.

On the other hand, the cost of killing males may turn out to be negative in some cases, especially in highly polygynous species. Fertilisation is then less dependent on sex ratios, whereas the presence of males may have a strong negative impact on female breeding success, i.e. $B'_M \ll 0$. This may happen through direct harassment and disturbance of females instead of, or in addition

to, competition for resources.

Considering equations in Table 1, one should also note the possibility of a trade-off between S and B , in that short-lived species lay larger clutches (Zammuto 1986, but *see* Arnold 1988). However, this is not necessarily true, since S incorporates summer survival only, and it may stay near 1 regardless of B if most of the mortality occurs during winter (as in male but not female mallards in Blohm *et al.* 1987).

The magnitude of the density-dependent compensatory responses during summer, $(S_M)'$, $(S_F)'$, and B' , is much harder to determine than values S_M , S_F and B themselves. The overall annual degree of compensation is already hard to estimate (Barker *et al.* 1981, Nichols & Hines 1983, Burnham & Anderson 1984, Hill 1984, Nichols *et al.* 1984, Reynolds & Sauer 1991, Rexstad 1992, Smith & Reynolds 1992, 1994, Sedinger & Rexstad 1994, Williams *et al.* 1996), let alone the partitioning of it to specific seasons and to the effects of different sexes. Here, our predictions remain largely theoretical. Density dependence at some stage is required to maintain a persistent population (Royama 1992), but this does not necessarily require that any of the six summer responses $(S_M)'_F$, $(S_M)'_M$, $(S_F)'_F$, $(S_F)'_M$, B'_F or B'_M deviate from zero. If the population is regulated in winter conditions (such that winter survival decreases with density at least for females, $(W_F)' < 0$) any summer compensation does not necessarily need to exist. This would mean the highest cost for spring hunting, as compensation in the summer reduces the costs. However, if winter survival is largely density-independent, we would expect some compensation in at least some of the summer responses. Many of the compensatory responses are of the form $N \times S'$, where N is the number of individuals, and S' is the decrease in per-capita survival by an addition of one individual. Comparing this to the cost of the removal of the individual itself, the compensation is complete only if $|N \times S'| = S$. This means that to reduce the cost to 0, the removal of one individual should cause a sufficiently high increase in the survival of others such that the adult population at the end of the season remains unaffected by the original removal of one individual. Similar criteria apply for the breeding response B' .

Sex-specific compensation is difficult to study, but numerical examples of the costs show that relatively small compensatory responses in the summer do not markedly change the outcome from assuming no compensation (Fig. 2). Instead, the parameters α , the fraction of paired individuals of the minority sex, and β , the breeding success of unpaired females, are important. The cost of killing a male in spring is highest if the probability that it was mated is high, and if the breeding success of widows is low (Fig. 2). In some settings, the cost of killing a male can even exceed that of killing a female, since β affects male and female costs differently. Killing of females is most costly if β is high, since then the breeding output will be reduced much, whether or not the female was paired. Increasing α increases costs of killing females if $\beta < 1$, as it increases the average breeding output which is then lost by killing the female. Surprisingly, whether or not killing of a male occurs before or after pair formation does not necessarily have a large effect on the cost: if males are in short supply (female-biased sex ratio), both cases are equally costly, and if they are not (male-biased sex ratio), the probability that the male was paired is reduced, rendering his effect on population growth mild (Fig. 2). Also, it should be noted that even in cases where the male does not contribute much to population growth, its absence from the autumn bag is always present as a 'baseline' cost.

The study of Hario *et al.* (1995) on common eiders in southern Finland provides hitherto the only estimate of $\beta \approx 0.5$. Timing II was used in this study. With most females being paired, and female success being halved in widows, the point $(\alpha, \beta) \approx (1, 0.5)$ seems reasonable. Both surfaces that use timing II of male killing (Fig. 2) indicate $C_M > 1$, if male survival in summer is reasonably high and if density dependence operates mainly during winter instead of summer. It is thus wholly possible that spring hunting in males reduces the sustainable autumn bag more than its immediate benefits yield. A potential conflict of interest is, of course, that in migratory birds the spring and autumn bag are obtained in different countries. As an example, the spring hunting of male eiders in Finland affects a population that winters in Denmark and is harvested there from the 1 October (Noer *et al.* 1995).

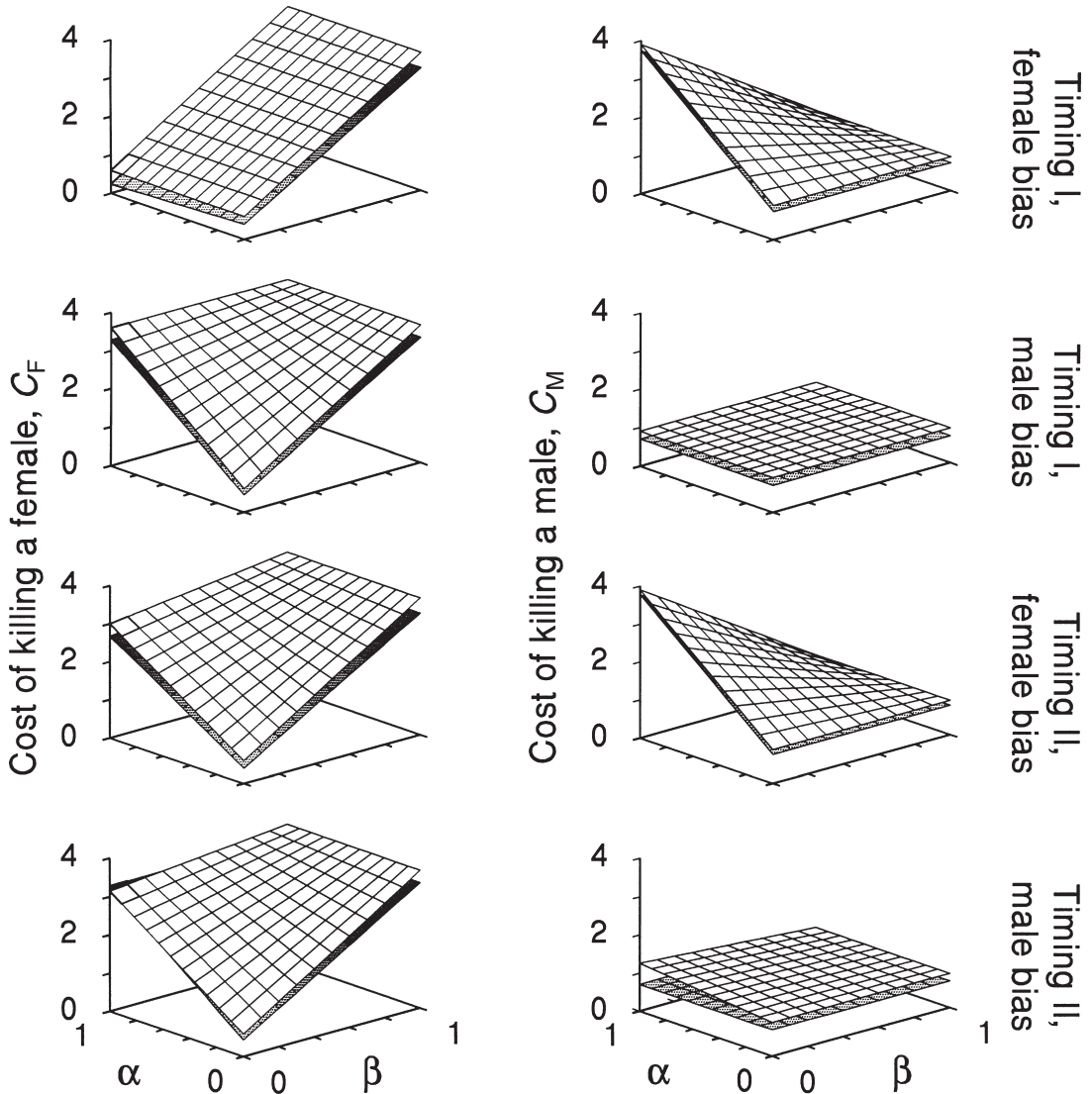


Fig. 2. An example of the costs (Table 1) as a function of α , proportion of paired individuals, and β , the breeding success of unpaired females in relation to that of paired ones. Upper surface gives the cost if there is no compensation in the summer (i.e., all derivatives in Table 1 equal 0), and the lower shaded surface gives the cost if compensation occurs within the same sex but not between sexes (e.g., if habitat use differs in the two sexes): $B'_F = (S'_F)'_F = (S'_M)'_M = -0.000\ 02$. Spring population sizes are assumed to be 8 000 individuals in the minority sex, 10 000 individuals in the majority sex, and breeding output is $\beta = 3$. The slopes of density dependence imply a compensation of 16%...20% in both mortality and (in case of a female killed) in the loss of broods, depending on which sex is the majority sex. Summer survival equals $S_F = 0.6$ for females and $S_M = 0.9$ for males. The cases are drawn assuming current spring harvesting pressure of 1 500 males and no females, but the outcome regarding cost per individual is not very sensitive to changing this assumption. Note that the assumption of no killing of females still allows to calculate a cost per killed female; this refers to the cost of accidental killing of a female mistaken as a male, if the planned 'baseline' female bag equals 0.

5. Discussion

It is not surprising that our results suggest generally a greater cost of hunting females than males.

Costs of male hunting are limited (though not necessarily 0), if males are the surplus sex in spring, if hunting occurs prior to pair formation, and if male hunting does not render the sex ratio female-

biased again. However, some parts of our results also imply conflicting results: if habitat use differs in summer among sexes, it suggests 'safe' harvesting of males as it is unlikely that the presence of these males is necessary for female breeding success, but it also prevents a compensatory response in female survival or breeding success.

High summer survival of either sex increases the cost both directly, and because it suggests limited space for a strong density-dependent compensation. Similarly, a large reduction in breeding success for widowed or unpaired females (low β) implies a high direct cost and a smaller potential for cost reduction through breeding compensation. The same logic applies if being paired is the rule (high α). Thus, long-lived species with biparental care are naturally very vulnerable to spring hunting, but problems of fertilisation may lead to the same result even if all subsequent breeding effort is done by the female (Hario *et al.* 1995). In short-lived species, on the other hand, breeding output B is likely to be high as a result of the equilibrium dynamics. Whether or not S is high as well depends on the timing of natural mortality.

Our model makes some simplifying assumptions, such as neglecting any age structure that might affect breeding success, survival, and vulnerability to hunting. Many of the parameters in our model are very difficult to obtain estimates for, as the compensatory or additive nature of hunting mortality is difficult to estimate even on an annual scale (e.g., Nichols *et al.* 1984). One should also be aware of the possibility that habitat availability, and not the spring number of individuals, sets a limit to the number of breeding pairs P , as this will lead to a large fraction of non-breeding 'floaters' whose killing will have little effect on the reproduction of the population (Kokko & Sutherland 1998). Effects of spring hunting in such a case would depend on how much harvesting can be focused on the non-breeding fraction, and on whether or not a breeding individual will be replaced by a floater during the same breeding season.

Naturally, it is dangerous to rely on models without biological justification (Johnson *et al.* 1985). However, we attempted here to encompass the extremes that might be possible in nature, and show some general directions in which e.g., compensation or different habitat usage can lead the results. The results should be used as rough guide-

lines in determining in which cases the effects of spring harvesting are likely to be stronger or weaker; also, they suggest what parameter estimates would be needed most to get a more accurate picture of the true cost. Average breeding output and survival during summer are important as they give the maximum cost surface (Fig. 2) assuming no compensation. Further, knowledge of spring sex ratios and information on the frequency and breeding success of unpaired individuals would enable distinguishing between cases of Fig. 2 more accurately. Finally, costs will be reduced if density dependence compensates for losses during summer, and estimating the magnitude of the reduction would mean estimating seasonal density dependence.

In general, our detailed model gives the impression that the simple wisdom of 'not to deduct from the capital' does hold, even for males if pairing is important, and then even for harvest timing prior to pair formation if there is a danger that spring sex ratios become female-biased as a result of selective culling of males. However, no alternative of the model yields a full cost of $(1 + B)$, i.e. one individual and its subsequent B offspring, because of density-dependent and density-independent effects of summer survival, pair formation and reproduction. Depending on these details, the cost may in some cases remain below one autumn individual especially for males, in which case some economic benefit may be assigned to spring hunting. Whether or not spring hunting is then considered harmful depends on other factors not considered here, e.g., the disturbance caused to breeding females of the same species or to wildlife in general when hunting at the onset of the breeding season when resources are at critical levels (Madsen & Fox 1995). The overall outcome, however, confirms that even if such considerations are omitted and the economic side (counted as the total hunting bag) is the only criterion in use, the population-wide cost of spring hunting can reduce the autumn benefit much more than its gain in the spring can compensate for.

Acknowledgements: We thank Tapani Veistola for discussion and for providing background information, and Jesper Madsen and an anonymous referee for constructive comments. This study was funded by the Academy of Finland, the Maj and Tor Nessling Foundation, and the Emil Aaltonen Foundation.

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