The effects of harvest on waterfowl populations

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Abstract

Change in the size of populations over space and time is, arguably, the motivation for much of pure and applied ecological research. The fundamental model for the dynamics of any population is straightforward: the net change in the abundance is the simple difference between the number of individuals entering the population and the number leaving the population, either or both of which may change in response to factors intrinsic and extrinsic to the population. While harvest of individuals from a population constitutes a clear extrinsic source of removal of individuals, the response of populations to harvest is frequently complex, reflecting an interaction of harvest with one or more population processes. Here we consider the role of these interactions, and factors influencing them, on the effective harvest management of waterfowl populations. We review historical ideas concerning harvest and discuss the relationship(s) between waterfowl life histories and the development and application of population models to inform harvest management. The influence of population structure (age, spatial) on derivation of optimal harvest strategies (with and without explicit consideration of various sources of uncertainty) is considered. In addition to population structure, we discuss how the optimal harvest strategy may be influenced by: 1) patterns of density-dependence in one or more vital rates, and 2) heterogeneity in vital rates among individuals within an age-sex-size class. Although derivation of the optimal harvest strategy for simple population models (with or without structure) is generally straightforward, there are several potential difficulties in application. In particular, uncertainty concerning the population structure at the time of harvest, and the ability to regulate the structure of the harvest itself, are significant complications. We therefore review the evidence of effects of harvest on waterfowl populations. Some of this evidence has focussed on correspondence of data with more phenomenological models and other evidence relates to specific mechanisms, including density-dependence and heterogeneity. An important part of this evidence is found in the evolution of model weights under various adaptive harvest management programmes of the U.S. Fish and Wildlife Service for North American waterfowl.

Overall, there is substantial uncertainty about system dynamics, about the impacts of potential management and conservation decisions on those dynamics, and how to optimise management decisions in the presence of such uncertainties. Such relationships are unlikely to be stationary over space or time, and selective harvest of some individuals can potentially alter life history allocation of resources over time – both of which will potentially influence optimal harvest strategies. These sources of variation and uncertainty argue for the use of adaptive approaches to waterfowl harvest management.

Key words: additive mortality, compensatory mortality, harvest, population structure.

Annual migrations of waterfowl have long provided human populations with a regular source of protein and outdoor recreation. Their use as a valuable quarry and food has been facilitated by the great concentrations of these birds at some wintering or migration stopover sites, the ease with which their eggs could be collected, and the flightless moulting period making adults particularly vulnerable to trapping during late summer. Not surprisingly, waterfowl remains are very common at prehistoric human settlement sites (*e.g.* Ericson & Tyrberg 2004), and antique artefacts of waterfowl hunting are numerous (*e.g.* Egyptian paintings or Roman mosaics; see Arnott 2007). Subsistence hunting of waterfowl is still a traditional activity, especially in the Arctic where some duck and goose species breed (Padding *et al.* 2006). Commercial harvest of waterfowl is also legal and heavily practiced in some parts of species wintering ranges (Balmaki & Barati 2006). However, much of current waterfowl harvest is now through recreational hunting. Because of their cosmopolitan distribution over both the northern and the southern hemisphere, there is virtually no area around the globe where there are wetlands and no waterfowl harvest of any type.

Throughout much of the world, and certainly in North America and Europe, there is widespread recognition that waterfowl hunting requires some form of regulation. This recognition reflects the assumption that unregulated harvest has the potential to reduce waterfowl populations to dangerously low levels. As a result, government organisations worldwide have imposed various restrictions on the hunting of waterfowl, including, for example, establishment of seasons of the year and times of day when hunting is not permitted, areas within which hunting is not permitted, daily limits to the number of birds that can be harvested, restrictions on types of baits and other attractants (*e.g.* types of decoys) that can be used, and restrictions on the number and types of shells permitted. These various restrictions represent management actions designed to bring about desired outcomes with respect to harvested waterfowl populations. Implementation of such restrictions thus pre-supposes knowledge of the relationships between these regulations and harvest rates, and between harvest rates and waterfowl population change. However, both sets of relationships are characterised by uncertainty. Some of this uncertainty is likely not resolvable. For example, the exact harvest rates that result from a specific set of hunting regulations are always likely to be viewed as random variables arising from a distribution that characterises this source of partial controllability (Johnson *et al.* 1993, 1997). However, the relationships between harvest rates and both waterfowl survival rates and population change are represented by competing hypotheses and thus by uncertainty that is potentially resolvable by evidence. These hypotheses are the focus of this review, as we consider available evidence and ways to provide further resolution as a means of improving future management of waterfowl resources.

Despite the relatively narrow focus of our review, we remind the reader that harvest regulation is one of a relatively large number of potential actions that can be used to manage waterfowl populations. For example, a variety of management actions has been developed to improve habitat on waterfowl breeding grounds. Some of these actions are very specific and local, such as erecting nesting structures for cavity nesting species (Hawkins & Bellrose 1940; Bellrose 1990), constructing islands as potential nesting sites with reduced access to predators (Hammond & Mann 1956; Giroux 1981), and planting dense nesting cover for prairie nesting species (Duebbert *et al.* 1981; McKinnon & Duncan 1999). Other actions, such as the Conservation Reserve Program (Reynolds *et al.* 1994, 2001), are much less specific, and are designed to influence habitat across broad geographic areas. Active control of nesting predators can be viewed as a form of breeding habitat improvement. Predator reduction has been successfully applied throughout the world (Garrettson & Rohwer 2001; Kauhala 2004; Whitehead *et al.* 2008; Pieron & Rohwer 2010); however, in many parts of the world (*e.g.* North America) controversy remains about whether this action should be considered. Management actions affecting migration and wintering habitat have also been identified and implemented for waterfowl (Gilmer *et al.* 1982; Smith *et al.* 1989). In summary, a variety of potential management actions exists, and integrated programs of waterfowl management should include consideration of multiple actions (including harvest regulations) in order to achieve programme objectives (Runge *et al.* 2006).

History of waterfowl harvest management

In North America prior to the mid-1800s, waterfowl were viewed as extremely abundant and accordingly were hunted for sale and recreation throughout the year (Phillips & Lincoln 1930; Day 1949). Population declines in the late 1800s and early 1900s led to concerns about effects of harvest and to the beginning of government intervention. The United States government was granted authority to regulate waterfowl harvest, and the Migratory Bird Treaty Act of 1918 specified that hunting would be permitted only when deemed compatible with protection and maintenance of populations. During the period 1930–1950, the perception of declines and low populations led to restrictions in hunting regulations (U.S. Fish and Wildlife Service 1988) and to the initiation of monitoring programmes designed to assess waterfowl population status (Martin *et al.* 1979; Smith *et al.* 1989; Nichols 1991a). Over the next 25 years, these monitoring programmes were expanded and improved, and resulting data were employed to develop population models for use in establishing harvest regulations for key species (Crissey 1957; Geis *et al.* 1969). During this period (1951–1975), these models and conventional wisdom led to restriction of hunting regulations during years when breeding grounds were dry and population sizes low, producing disagreements about the effectiveness of such restrictions and the perceived lack of consideration of the desires of the hunting public (Nichols 2000). However, these political disagreements were not well-grounded in science, and the management of waterfowl hunting in North America was generally viewed as a good example of the scientific management of animal populations (Nichols *et al.* 1995).

In the early 1970s, analyses of Mallard *Anas platyrynchos* ringing and recovery data, using newly developed inference methods, led Anderson & Burnham (1976) to the conclusion that historical data did not provide strong support for the premise that had guided Mallard harvest for the prior 50 years, that changes in Mallard harvest rates had produced corresponding changes in Mallard survival and population size. This landmark study introduced structural uncertainty to North American waterfowl harvest management; that is, uncertainty in hypotheses about how changes in waterfowl harvest translate into changes in population dynamics. Subsequent efforts to resolve this uncertainty and manage waterfowl harvest in the face of it include a period (1979–1985) of stabilised hunting regulations (McCabe 1987) and a subsequent period (1985–1990) of risk-aversive conservatism (Sparrowe & Patterson 1987; U.S. Fish and Wildlife Service 1988). However, neither of these approaches led to resolution of the uncertainty, nor to a widely accepted approach for dealing with it.

In the early 1990s, members of the Office of Migratory Bird Management, U.S. Fish and Wildlife Service (USFWS), began to give serious consideration to implementing an adaptive approach to harvest management. Although the central ideas underlying adaptive management had been described and developed by Walters (1986), the approach had never been fully implemented on even a small scale. In 1992, Fred Johnson of the USFWS assembled an *ad hoc* working group of state and federal waterfowl biologists to discuss alternative approaches for waterfowl harvest management. The ideas of adaptive harvest management (AHM) were discussed, and the group decided to develop this approach, becoming the interagency working group for AHM. The proposed approach to AHM was outlined in Johnson *et al.* (1993) and formally adopted by the USFWS for mid-continent Mallard in 1995 (Nichols *et al.* 1995; Williams & Johnson 1995; Johnson *et al.* 1997). AHM was especially attractive because it provided a means of simultaneously reducing uncertainty while managing in the face of it. The AHM programme for mid-continent Mallard is still used each year to establish recommended hunting regulations. Its success has led to the development of AHM programmes for other Mallard populations and other waterfowl species in North America (*e.g.* Atlantic Flyway Canada Geese *Branta canadensis*; Hauser *et al.* 2007). Inferences reviewed in this paper about the relationship of hunting regulations and harvest rates to waterfowl populations are based both on specific analyses and on the results of AHM programmes.

The general pattern of increasing protection of waterfowl and regulation of harvest has occurred in Europe as well, where waterfowl were also considered as an almost infinite resource until the end of the 19th Century, and were commercially exploited as such. Duck decoys, in particular, were used to trap birds at their wintering and migration stopover sites, sometimes in an industrial manner (33,000 teal were caught in a single season on one island in the North Sea, leading to the building of a duck canning factory; Phillips 1923). Such commercial harvests gradually lost popularity and were abandoned throughout Europe during the 20th century, although trade of legally-harvested waterfowl by recreational hunters is still legal in some countries. Because of the number of different countries in Europe, it is more difficult to reach international agreements, and national waterfowl management policies have sometimes developed towards different systems and at different paces. The main current legal framework is the 'Bird Directive' (adopted by the European Commission in 1979), which limits in particular the periods of the year during which birds can be harvested anywhere along their flyways, and the African-Eurasian Waterbird Agreement (AEWA), which aims to coordinate research, monitoring and policy at the Palearctic flyway scale (including beyond the European Union). The European waterfowl management policy is therefore far less developed than the American system, although the eventual set-up of a proper international adaptive harvest management scheme is a goal for the future (Elmberg *et al.* 2006). In fact, an adaptive management programme for the Svalbard Pink-footed Goose *Anser brachyrynchus* population is under current development (*e.g.* Johnson *et al.* 2014).

Life history characteristics of waterfowl

Despite the general similarities in morphology and behavioural habits, waterfowl form a very diverse family of birds when it comes to body size, with up to a 32-fold difference in body mass between a 330g Green-winged Teal *Anas carolinensis* and a 10.5 kg Trumpeter Swan *Cygnus buccinator*. Such differences in body mass have obvious consequences in terms of, for instance, energy needs (Miller & Eadie

2006), which translate into very different life history strategies. These differences have long been recognised, as exemplified in the following statement from the mid-20th century: "Another inference from the general observation that geese are bigger than ducks is that large waterfowl survive better, and produce fewer offspring, than small ones" (Boyd 1962).

Waterfowl therefore can be broadly organised along a "fast-slow" gradient, with faster duck species having short life expectancies but a high annual reproductive output, as opposed to slower geese and swans surviving much longer but producing fewer offspring per breeding attempt (Gaillard *et al.* 1989). In line with ducks producing more offspring which survive more poorly, density-dependent feedback on individual survival is thought to be more common in ducks, at least during some stages of their life cycle (Gunnarsson *et al.* 2013), while this is not so much the case in geese and swans. Life history variation exists even within ducks (subfamily *Anatinae*). For example, among North American ducks, Patterson (1979) characterised Mallards, Blue-winged Teal *Anas discors*, and Northern Pintail *Anas acuta* as relative "*r*-strategists" (faster life histories) and Redhead *Aythya americana*, Canvasback *Aythya valisineria* and Scaup *Aythya marila* as "*K*-strategists" (slower life histories).

The constraint imposed by their smaller size prevents ducks from carrying substantial body reserves along long migratory flights (Klaassen 2002), leading to their characterisation as "income breeders"; *sensu* Drent & Daan (1980), in that they mostly rely on the energy available at or near their breeding grounds to fuel their reproduction. In contrast, the larger size of geese and swans permits the storage of lipid and protein reserves well before reproduction, often as early as on the wintering grounds, leading to their characterisation as "capital breeders". Such differences in life history strategies have profound consequences for population structure and, hence, the modelling of population dynamics. Duck populations are generally considered as being relatively simple in structure, with little need to incorporate age structure beyond the first-year/adult dichotomy (Devineau *et al.* 2010). Conversely, the low reproductive rate and long survival of geese, swans and many sea ducks lead to more complex populations, with delayed age of first breeding, extended age-specificity, *etc.* The greater heterogeneity among individuals within such populations often requires the use of more structured models.

Modelling considerations: structure & heterogeneity

Models are used in harvest management to allow us to predict the numerical response of a population subjected to a certain level of harvest. However, all population models, regardless of their application (*e.g.* harvest management), represent approximations to reality which can never be fully specified. Utility of the model in the context of harvest management is primarily determined by the degree to which the model correctly represents the functional form relating the management control option (say, varying harvest pressure through legislative action), and the response of the population to harvest. Much literature has focussed on the question of whether harvest mortality in waterfowl is "additive" or "compensatory" to natural mortality (see below), and the impacts of that distinction on optimal harvest management. Second, the ability of a population model to reflect accurately the dynamics of a population will be strongly influenced by the degree to which the model structure adequately accounts for important differences among individuals, both in terms of underlying vital rates (survival, fertility), but also potentially in the functional response of those vital rates to perturbation (*i.e.* harvest). At one extreme, simple scalar models assume that all individuals have identical latent probabilities of survival and reproduction – we refer to such models as *scalar projection models*. As noted in the preceding section, for many duck populations, such simple scalar or near-scalar models are often sufficient. At the other extreme, we imagine a model containing sufficient structure to model the dynamics of each individual in the population. We refer to such models as *individually-based projection models*. It is clear that this latter class of models represents the closest approximation to full reality. Such a model would completely account for heterogeneity among individuals in the population (the role of individual heterogeneity will be re-visited later).

However, a fully individually-based population model is generally intractable, both in terms of construction, analysis and application in a management context. For example, estimation of a time-specific survival probability for individual i over time step t to $t + 1$ requires inference about a binomial parameter based on a single Bernoulli trial. Based on whether the individual is alive or dead at time $t + 1$, we must somehow estimate the underlying probability of survival, and there is simply not enough information in this single observation to allow us to do this well (see Cohen 1986). As such, we are generally left constructing a model which represents a compromise between a simple scalar model, and a fully individually-based model. Such "intermediate" models are based on the reasonable idea that much (if not all) of the variation among individuals can be explained by one or more factors (demographic, genotypic, spatial, developmental), which can be used to structure a population into (generally) discrete classes of individuals grouped together by sharing one or more of these factors (we note that in some cases, discretization is a mathematically convenient approximation to the continuous state-space). For many waterfowl species, particularly longer-lived swans and geese, and many sea ducks, there is significant variation in both survival and fertility as a function of the age of the individual. A model which differentiates among individuals based on differences in such factors is known generally as a *structured model*. Such models are parameterised not only in terms of potential differences in survival and fertility among classes of individual, but also in terms of the probability of making transitions among classes (due to aging, growth or movement).

This section addresses the impact of population structure on the projected impacts of that harvest on waterfowl population dynamics; we defer consideration of the role of different functional forms relating harvest to the numerical response to the next section. Here, we describe the conditions under which harvest would lead to change in population abundance, and the structural factors influencing the magnitude and time course of such change.

Equilibrium harvest for scalar populations

We introduce some of the basic considerations in model-based harvest management through a numerical example. We consider first a simple deterministic scalar population in discrete time, without density-dependence, where the population size N at time $t + 1$ is given as the product of the current population size at time t and a scalar multiplier, λ.

$$N_{t+1} = \lambda N_t . \tag{1}$$

As long as $\lambda > 1$, then $N_{t+1} > N_t$ (*i.e.* the population will grow). In the absence of harvest or some other "control" measure, the population will grow without bound. In such cases, we focus on calculating the equilibrium harvest rate, E, which represents the maximum harvest which does not lead to the increase or decline of the population over time (*i.e.* the harvest condition under which $N_{t+1}/N_t = 1$):

$$\frac{N_{t+1}}{N_t} = (\lambda - E). \tag{2}$$

Thus, for example, a population with $\lambda = 1.05$ is projected to grow at 5% per time step. The equilibrium harvest rate then is simply $E = (1.05–1) = 5\%$. In terms of absolute numbers, if $N_t = 1{,}000$, then the equilibrium harvest would be 50 individuals at each time step.

Equilibrium harvest for structured populations

Now we consider a structured population. While there are a number of different classes of structured models, we will focus on the use of matrix-based models, which are canonical models for discrete-time population dynamics, where individuals are classified (grouped) into discrete "(st)ages" (Caswell 2001; Lebreton 2005). To simplify the presentation, we will consider deterministic models, with no density-dependence. We'll assume the minimal structured model with 2 age classes (juveniles and adults, where the adult class consists of all individuals ≥ 1 years of age). Fertility and survival transitions for our example population are given in the life-cycle graph shown in Fig. 1 (constructed assuming a post-breeding census; Caswell 2001). Assuming $S_A = 0.65$, $S_J = 0.5$, and $F = 0.8$, then the projection matrix model **A** can be constructed directly from the life-cycle graph as

$$\mathbf{A} = \begin{bmatrix} S_J F & S_J F \\ S_J & S_A \end{bmatrix} = \begin{bmatrix} 0.40 & 0.52 \\ 0.50 & 0.65 \end{bmatrix}, \tag{3}$$

from which we derive the following standard metrics for projected growth (λ), stable age proportions (w_i), and age-specific reproductive values (v_i; for details see Caswell 2001):

$$\lambda = 1.05, \mathbf{w} = \begin{bmatrix} 0.3478 \\ 0.4348 \end{bmatrix}, \mathbf{v} = \begin{bmatrix} 1.0 \\ 1.5 \end{bmatrix}.$$

Thus, in the absence of harvest and assuming time-invariance and no density-

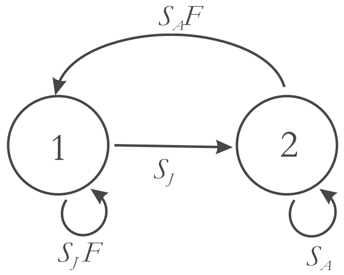

Figure 1. Life-cycle graph and structure of the underlying life history for the 2-age class (adults, juveniles) example. The life-cycle graph is based on a post-breeding census. Node 1 is the number of juveniles (offspring) in the population, and node 2 is the number of adults (age ≥ 1 year). The arcs connecting the nodes reflect survival (left-to-right) and fertility (right-to-left). S_A and S_J are the survival probabilities for adults and juveniles, respectively. F is the reproductive rate, and is assumed to be invariant with age for age > 1 year.

dependence, the population is projected to grow without bound at 5% per time step, eventually stabilising at a juvenile:adult ratio of 4:5. As indicated by the reproductive value vector **v** (Fisher 1930), each adult in the population is worth 1.5 juveniles to future population growth, suggesting that harvest of an adult individual is potentially of greater impact than harvest of a juvenile individual. (Here, we have normalised **v**, and **w** so that **v'w** = 1. It is customary to express **v** such that $v_1 = 1$, so that the reproductive value of each stage is compared to that of the first stage, and **w** such that the elements w_i sum to 1, so they represent the proportion of the population in each stage class).

The difference in reproductive value between adults and juveniles represents a key consideration which differentiates modelling the harvest of a structured population, and harvest of a simple scalar population. Reproductive value is a well-known concept in evolutionary biology (Stearns 1992 provides a general review) and has been identified as affecting the optimal age- or stage-specific harvest of a population (MacArthur 1960; Grey & Law 1987; Brooks & Lebreton 2001; Kokko 2001; Lebreton 2005; Hauser *et al.* 2006). Harvest of individuals of higher reproductive value will, generally, have a greater proportional impact on population dynamics than harvest of individuals with lower reproductive value (although the relative value of individuals may change following a perturbation (Caswell 2001; Cameron & Benton 2004) and is a function of whether or not the population is increasing or decreasing at the time of harvest (Mertz 1971)). Thus, the inclusion of structure adds extra dimensions of uncertainty, but also additional flexibility and opportunities, to harvest management. Most obviously, a structured model may require a structured harvest to reach an optimal harvest objective.

Constant harvest

We can demonstrate the role of structure and age-specific reproductive value by means of a simple numerical example. Suppose at time t the population consists of ~1,000 individuals. Based on a simple scalar model, a projected growth rate of $\lambda = 1.05$ (as per the preceding example) implies that we could harvest at most 5% of the population each time step. Given, say, 1,000 individuals in the population at the time of harvest, this would correspond to a constant harvest of 50 individuals.

But, which 50 individuals? Juveniles, adults, or some of each? Consider the 2-age-class structured model introduced earlier (eqn. 3), and the consequences of harvesting 50 juveniles, *versus* harvesting 50 adults from a starting population of ~1,000 individuals (assuming for the moment that we could selectively harvest a particular age class – the implications of violating this assumption are considered later). If the population structure at the time of the harvest is proportional to the equilibrium age structure (*i.e.* consisted of 444 juveniles, and 555 adults), then the population – and thus each age class – is projected to increase at 5% per time step. Under these conditions, it might seem reasonable to assume that harvesting 50 adults, or 50 juveniles, or any vector summing to 50 total individuals (*e.g.* 25 adults and 25 juveniles), would have the same effect on long-term dynamics (namely, no change in population size between now and the next time step following harvest). However, this is not the case – in fact, the direction and magnitude of the change in the population is determined by the relative proportions of each age class in the harvest.

Since such a result might seem counter-intuitive, it is useful to evaluate the correct equilibrium harvest conditions for a structured population. Let the dynamics of a structured population subjected to a constant harvest be given by:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t - \mathbf{E}, \qquad (4)$$

where **A** is the matrix projection model, and **E** is the harvest vector where the *i*th element represents the number of individuals in stage *i* that is harvested during each time period (here, we assume a specific, constant number of individuals harvested for each age class. We consider proportional harvest later). Under equilibrium harvest for a discrete-time projection model, $\mathbf{N}_{t+1} = \mathbf{N}_t = \mathbf{N}^*$. Thus, eqn. (4) can be rearranged to show that:

$$\mathbf{N}^* = (\mathbf{A} - \mathbf{I})^{-1}. \qquad (5)$$

If **A** is primitive (which is generally the case for population projection models, which are generally positive and square), then the unharvested population will eventually grow as:

$$\mathbf{N}_t \sim (\mathbf{v}'\mathbf{N}_0)\lambda^t\mathbf{w}.$$

Following Hauser *et al.* (2006), if the difference between the harvested population and the equilibrium state after some time *t* is:

$$\mathbf{N}_t - \mathbf{N}^* \sim [\mathbf{v}'(\mathbf{N}_0 - \mathbf{N}^*)]\lambda^t\mathbf{w}, \qquad (6)$$

then the equilibrium harvest vector **E** is given as:

$$\mathbf{v}'\mathbf{E} = \mathbf{v}'[\mathbf{N}_0(\lambda - 1)]. \qquad (7)$$

Now (λ–1) is the long-term proportional increase of the unharvested population (*e.g.* if $\lambda = 1.05$, then the population will increase by (1.05–1) = 5% per year in the long term). The reproductive value of this 'excess' proportion of the initial population $\mathbf{N}_0$ (the right-hand side of eqn. (7) must be equal to the reproductive value of the harvest (the left-hand side of eqn. (7). This ensures that the harvest is sustainable and that the population will approach a steady state over time.

Returning to our numerical example, if the initial population $\mathbf{N}_0$ is known, then we find harvest vectors **E** that satisfy the equilibrium condition (eqn. 7). The initial population may have the stable stage distribution of the unharvested system, *e.g.* $\mathbf{N}_0 = (444{,}555)'$. Then:

$$\begin{bmatrix} 1.0 & 1.5 \end{bmatrix} \begin{bmatrix} E_J \\ E_A \end{bmatrix}$$

$$= (1.05-1)\begin{bmatrix} 1.0 & 1.5 \end{bmatrix} \begin{bmatrix} 444 \\ 555 \end{bmatrix},$$

leading to:

$$E_J + 1.5E_A = 63.825,$$

where E_J and E_A are the numbers of juveniles and adults harvested per time step, respectively. The equilibrium condition (eqn. 7) is that a particular linear combination of the harvest taken from each class is held at a constant. It is important to note that the coefficients for harvest from a class (*i.e.* E_J, E_A) are the reproductive values of individuals in those classes (*i.e.* $v_1 = 1.0$ for E_J, $v_2 = 1.5$ for E_A). The constant (in this case 63.825) is dependent on the initial population size and structure $\mathbf{N}_0$. The particular solution to the equilibrium harvest equation for our present example, where $\mathbf{N}_0 = (444{,}555)'$, is shown in Fig. (2). If the harvest $\mathbf{E} = (E_J, E_A)'$ that is actually taken falls below this line, then the population will eventually increase. If the harvest falls above this line then the population will eventually decline. Harvest that falls on this line (*i.e.* satisfying the equilibrium condition) will cause the population to stabilise over time to a population size and structure given by equation (7). We introduced this example by claiming that a total harvest of 50 individuals would cause the population to increase or decrease over the long term. We see clearly from this figure that a harvest of 50 adults only, and no juveniles, is above the line, leading to a population decrease. In contrast, a harvest of 50 juveniles only, and no adults, is below the line, leading to a population increase.

Note that the structure and size of this steady state population (*i.e.* at equilibrium) are dependent on the particular harvest vector $\mathbf{E}$ that is used. For example, if we choose to harvest only adults then the equilibrium population size is calculated to be > 1,000 (*i.e.* above the starting population size):

$$\mathbf{E} = \begin{bmatrix} 0.00 \\ 42.55 \end{bmatrix} \text{and } \mathbf{N}^* = \begin{bmatrix} 464.2 \\ 541.5 \end{bmatrix} = 1005.7.$$

If instead we choose to harvest only juveniles, the equilibrium population size is calculated to be < 1,000 (*i.e.* below the starting population size), then:

$$\mathbf{E} = \begin{bmatrix} 63.83 \\ 0.00 \end{bmatrix} \text{and } \mathbf{N}^* = \begin{bmatrix} 406.2 \\ 580.2 \end{bmatrix} = 986.4.$$

Three important points should be noted here. First, as mentioned earlier, the coefficients for harvest from a given age-class (*i.e.* E_J, E_A) are the reproductive values of individuals in those classes (*i.e.* $v_1 = 1.0$ for E_J, $v_2 = 1.5$ for E_A). In other words, the equilibrium harvest of juveniles only (63.825) would need to be 1.5 times larger than the equilibrium harvest of adults only (42.550; 63.825/42.550 = 1.5). This is because the harvest of a single adult from the population is demographically equivalent to the harvest of 1.5 juveniles. This linear relationship between the reproductive value vector and the equilibrium harvest vector is not limited to simple 2-age class models – for any number

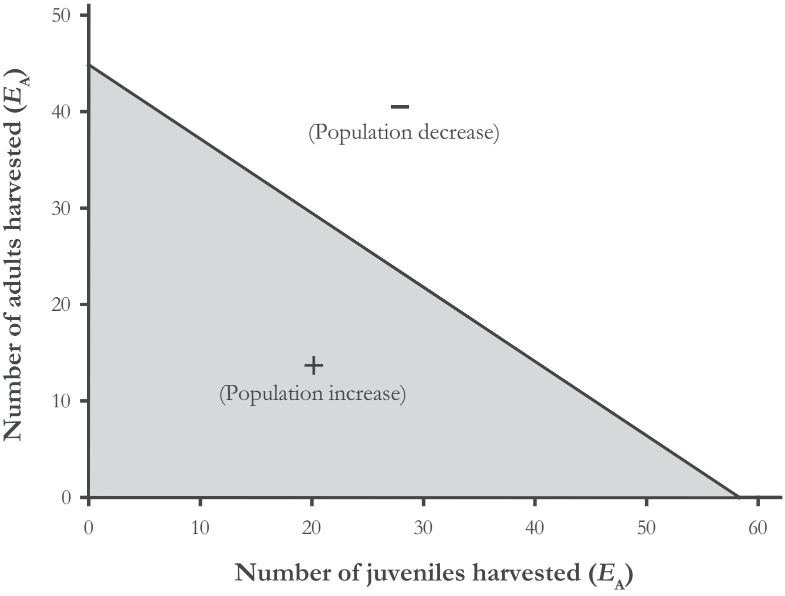

Figure 2. Equilibrium harvest for constant harvest of a fixed number of adults (vertical axis) and juveniles (horizontal axis), for the population projection model described by eqn. (3). The equilibrium harvest is specific to the initial population size and structure, which here we assume to be 1,000 individuals in the stable age proportions (*i.e.* $\mathbf{N}_0 = (444{,}555)'$). Harvest at any point below the equilibrium (shaded area) will cause the population to increase, whereas harvest at any point above the equilibrium will cause the population to decrease. Adapted from Hauser *et al.* (2006).

of age classes (≥ 2), the equilibrium expression is a *k*-dimensional plane, for *k* age classes in the model (Hauser *et al.* 2006; for most long-lived waterfowl species, $k \geq 5$). The coefficients of equilibrium solution are the reproductive values of the corresponding age classes.

The second point is that the population size at equilibrium is smaller for a juvenile-only harvest (986.4), and more skewed towards adults, compared to an adult-only harvest (1,005.7, 46% juvenile). This dependence of the final size and structure of the population on the structure of the population at the time of the harvest, and the structure of the harvest itself, is an important consideration addressed later (see also Koons *et al.* 2014a).

Finally, it is possible that the population does not stabilise at equilibrium abundance, but instead grows unbounded, even if the harvest satisfies eqn. (7). This can occur if in some time steps the number of individuals that needs to be removed for a given age class is larger than the number of individuals existing in that age class at that time. In such cases, the full "equilibrium harvest" cannot be taken, and the population grows unbounded (Hauser *et al.* 2006). (This issue does not occur if we implement a proportional harvest, as developed in the next section).

Proportional harvest

In the preceding, we considered a *constant* harvest, where a constant number of individuals is harvested (from a given age class) at each harvest decision. Such a scenario is arguably unrealistic for waterfowl harvest, where harvest regulations are based on an assumed relationship between various regulatory options and the proportional probabilities of mortality due to harvest (*i.e.* kill rate, K_t, the probability of being harvested during time interval t). Under *proportional* harvest, the same proportion of individuals is removed from each age class each time period (although the proportion may differ among age classes). The harvest model becomes:

$$\mathbf{N}_{t+1} = (\mathbf{I} - \mathbf{K})\mathbf{A}\mathbf{N}_t \,,$$

where $\mathbf{K} = \mathrm{diag}(K_1, K_2, \ldots, K_k)$, and $0 \leq K_i \leq 1$ is the proportion of age class i to be harvested. If harvest occurs immediately after reproduction (generally the case for waterfowl), then:

$$\mathbf{N}_{t+1} = \mathbf{A}(\mathbf{I} - \mathbf{K})\mathbf{N}_t \,. \qquad (8)$$

To find the equilibrium condition under proportional harvest, we again set $\mathbf{N}_{t+1} = \mathbf{N}_t = \mathbf{N}^*$, and solve for $\mathbf{N}^*$:

$$\mathbf{N}^* = \mathbf{A}(\mathbf{I} - \mathbf{K})\mathbf{N}^* \,. \qquad (9)$$

That is, we choose harvest vector $\mathbf{K}$ so that 1 is the dominant eigenvalue of $(\mathbf{I} - \mathbf{K})\mathbf{A}$.

We denote the corresponding right and left eigenvectors as $\mathbf{v}_K$ and $\mathbf{w}_K$, respectively. Then the population under harvest $\mathbf{K}$ will approach the equilibrium:

$$\mathbf{N}^* = \left(\mathbf{v}'_K \mathbf{N}_0\right)\mathbf{w}_K \,. \qquad (10)$$

We solve for $\mathbf{K}$ in a straightforward way. Using the matrix $\mathbf{A}$ from our 2-age-class model, then from eqn. (9):

$$\begin{vmatrix} -0.7 - 0.3K_J & 0.6 - 0.6K_J \\ 0.5 - 0.5K_A & -0.35 - 0.65K_A \end{vmatrix} = 0 \,,$$

which can be simplified to:

$$K_A = \frac{11 - 81K_J}{151 - 21K_J} \,,$$

which is a non-linear expression in K_A and K_J (although over the limited range of plausible values of $0 \leq K_i \leq 1$ for this problem, the equilibrium solution appears linear; Fig. 3). If the harvest chosen falls on this curve then the population will approach a steady state over time. If the harvest chosen falls below the curve then the population will grow geometrically over time. If the harvest chosen falls above the curve then the population will decline geometrically.

Two important differences should be noted compared to the constant harvest scenario introduced earlier. First, the equilibrium condition (eqn. 9) is not dependent on $\mathbf{N}_0$ (although the equilibrium population vector $\mathbf{N}^*$ is; eqn. 10), and is not a simple function of reproductive values (although it is clear from the equilibrium condition that a higher harvest rate for juveniles is required in order to achieve equivalence with a given harvest rate for adults, consistent with the interpretation of the relative value of juveniles and adults under a constant harvest model). Second, because we are dealing here with a proportional harvest, K_i, where $0 \leq K_i \leq 1$, then the situation where a full equilibrium harvest cannot be taken – as was the case

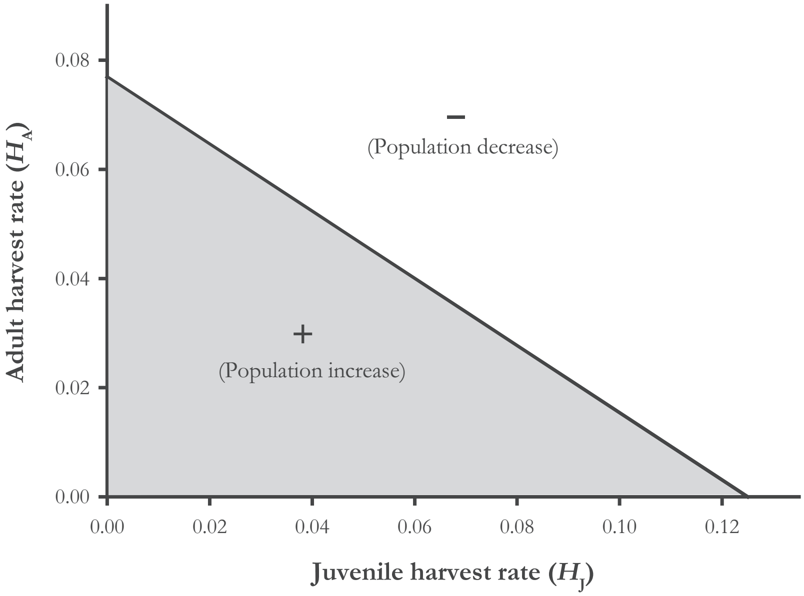

Figure 3. Equilibrium harvest for harvest of a fixed *proportion* of adults (vertical axis) and juveniles (horizontal axis), for the population projection model described by eqn. (3). The equilibrium harvest is specific to the initial population size and structure, which here we assume to be 1,000 individuals in the stable age proportions (*i.e.* $\mathbf{N}_0 = (444,555)'$). Harvest at any point below the equilibrium (shaded area) will cause the population to increase, whereas harvest at any point above the equilibrium will cause the population to decrease. Adapted from Hauser *et al.* (2006).

for a constant harvest if the equilibrium harvest for a particular age class was larger than the number of individuals in that age class – cannot occur. As such, under a proportional harvest, there is always a bounded equilibrium. However, as was the case for a constant harvest, the size and structure of the equilibrium population varies depending on both the structure of the harvest vector **K**, and the structure of the population at the time of harvest, $\mathbf{N}_0$ (Hauser *et al.* 2006). Since waterfowl harvest management is almost universally based on proportional harvest, we do not discuss constant harvest models further.

"Structure", by any other name…

In the preceding, we focussed exclusively on age structure (*i.e.* where the age of the individual was the only determinant of variation in survival or fertility among individuals specified in the model). For some species of waterfowl, especially longer-lived swans, geese and many sea ducks, age structure is clearly an important consideration.

However, while age structure may generally be a less important consideration for many short-lived duck species, there are other forms of structure which may be important considerations in model construction, some especially for ducks, and others for waterfowl generally (*e.g.* spatial structure). Brooks & Lebreton (2001) describe a simple application of the methods described in the preceding to a metapopulation, where the value of the individual is conditioned on both age and location. Further, the models presented above considered individuals of only one sex. While this may be appropriate in some cases, it may not always be the case, especially for species where the dynamics of the population are influenced by the form of the mating system (*e.g.* polygamy), or more commonly, where survival rates differ significantly between the sexes. In such cases, models where the dynamics of the two sexes are linked by the pair bond and maternity function are more appropriate. Such sex-linked models can generate rather complex dynamics (Caswell & Weeks 1986; Lindström & Kokko 1998).

Finally, all waterfowl populations (and wild populations in general) are characterised by differences among individuals that extend beyond the sources of variation already discussed. Even when models structurally separate males and females, or young and old, or one location *versus* another, within a given "node" (say, females of age 2, that are in location X), there are remaining differences among individuals. These differences are commonly referred to as reflecting "individual heterogeneity". While it is quite likely that these differences vary continuously among individuals, as a first approximation, we can consider modelling this additional heterogeneity (*i.e.* differences beyond those explained by structural elements such as age, or sex, or location) based on a finite set of "classes" of individuals (this is strictly analogous to the practice of using finite mixture models to approximate heterogeneity in analysis of mark-encounter data; *e.g.* Pledger *et al.* 2003). For example, consider a population where individuals can be characterised as either "high quality" or "low quality", based on their total latent survival probability (where a "low quality" individual is one with a lower probability of survival). In theory, we could reconfigure a matrix model which assumes that all individuals within a given structural class have identical latent vital rates (*e.g.* Fig. 1), to account for two discrete "quality" classes within that structural class. For example, if we assume that "quality" differences influence only juvenile and adult survival, but not fertility, then we might restructure the 2 age-class matrix model we considered earlier (Fig. 1) to reflect the unequal contributions of individuals of different quality to population growth (Fig. 4).

The projection matrix model **A** can be constructed directly from this life-cycle graph as:

$$\mathbf{A} = \begin{bmatrix} \pi S_{J,h}F + (1-\pi)S_{J,l} & S_{A,h}F & S_{A,l}F \\ \pi S_{J,h} & S_{A,h} & 0 \\ (1-\pi)S_{J,l} & 0 & S_{A,l} \end{bmatrix},$$

where $S_{x,q}$ is the latent survival probability of individuals of age class x, and quality class q (where q = *high* or *low*), F is the fertility rate, and π is the probability that a juvenile is (or will become) a "high" quality individual.

In this sense, heterogeneity models are (at least in simple, discrete form) structurally equivalent to models structured based on

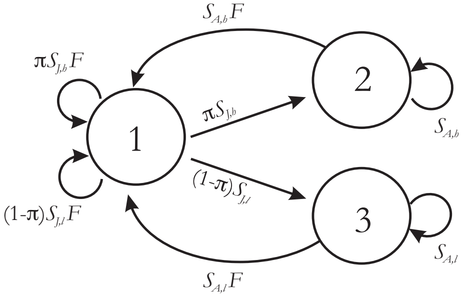

Figure 4. Life-cycle graph and structure of the underlying life history for a 2-age class (adults, juveniles) model, with discrete (finite mixture) heterogeneity in juvenile and adult survival. The life-cycle graph is based on a post-breeding census. Node 1 is the number of juveniles (offspring) in the population, and represents the combined fertility contributions of high quality (node 2) and low quality (node 3) adult (age ≥ 1 year) individuals, where differences in quality are characterised by lower juvenile and adult survival rates among lower quality individuals. The arcs connecting the nodes reflect survival (left-to-right) and fertility (right-to-left). $S_{A,q}$ and $S_{J,q}$ are the survival probabilities for adults and juveniles, respectively, for quality class q. The parameter π determines the probability that a new juvenile (node 1) becomes a high quality adult. F is the reproductive rate, and is assumed to be invariant with age and quality for age > 1 year.

age, location, or gender, and we can apply the same methods discussed earlier to evaluate the dynamics of the population described by this "heterogeneity" model to evaluate the relative value of harvest of individuals of low or high quality to those dynamics (*i.e.* reproductive value conditioned on both age and quality). The possible role of unspecified heterogeneity on numerical response to harvest is considered in a later section.

For some taxa (either sessile organisms, organisms that are temporarily sessile at the time of harvest – *e.g.* fish in the net in a commercial fishery, or where the mechanism of harvest is state-selective – *e.g.* use of nets of specific mesh size or other gear to capture only certain size-classes of fish), it is possible to harvest an individual selectively on the basis of its individual state (*e.g.* you keep the big ones, and toss back the small ones). For most waterfowl, however, there will often be considerable uncertainty in establishing the "state" of an individual at the time of harvest, and optimisation of harvest based on state structure of the population will be only partially controllable. Even in cases where the extent of uncertainty about system state is reduced (for example, if harvest occurs at locations where the targeted individuals represent specific age- or sex-classes), waterfowl harvest in many cases is simply a random selection of individuals with differential vulnerability to the harvest.

Consequences of hunting for waterfowl populations

As noted above, a key to making wise management decisions is to be able to make predictions about system response to potential management actions. For hunted populations, predictions will usually include the hunting mortality rate that will result from any prescribed set of regulations. Studies contrasting ring recovery rates in years of differing hunting regulations have provided evidence supporting the inference of higher harvest rates in years of more liberal hunting regulations (see reviews of

Nichols & Johnson 1989; Nichols 1991; Johnson & Moore 1996, and more recent species-specific evidence of Johnson *et al.* 1997; Francis *et al.* 1998; Calvert & Gauthier 2005; Alisauskas *et al.* 2011; Peron *et al.* 2012; Iverson *et al.* 2014). Of course numerous variables (*e.g.* environmental conditions and resulting migration timing, and regional hunter activity) in addition to hunting regulations are expected to influence hunting mortality rates. As a result, hunting mortality rates predicted to correspond to a specific set of hunting regulations are best characterised as a probability distribution. Examples of such distributions estimated for mid-continent Mallard and Black Duck are provided by Johnson *et al.* (1997) and USFWS (2013), respectively.

In addition to predicting the hunting mortality rate, predictions are required for the changes in survival rates (probability of surviving all mortality sources), reproductive rates, and the rate of movement in and out of the focal population expected to accompany this level of hunting mortality. Much of the uncertainty in waterfowl management involves these relationships, and most of the North American waterfowl programmes in adaptive harvest management include multiple models (and corresponding hypotheses) as a means of dealing with this uncertainty. We consider these relationships below.

Survival

The most direct influence of hunting mortality should be on the total (all sources) mortality rate. A general form for this relationship can be expressed as (eqn. 11):

$$E(S_t) = S_0(1 - \beta K_t), \qquad (11)$$

where E denotes expected value, S_t is the probability that a bird alive at the beginning of the hunting season in year t survives and is alive at this same time the next year ($t + 1$), S_0 is the probability that a bird alive at the beginning of the hunting season in year t would survive to that same time the following year $t + 1$ in the complete absence of any hunting mortality, K_t is the probability that a bird alive at the beginning of the hunting season in year t would die from hunting causes before that same time the following year $t + 1$ in the complete absence of any non-hunting mortality, and β is the slope parameter relating S_t and K_t.

Equation (11) is very general and can be used to model a variety of relationships between hunting and survival depending on the value of β, with $\beta = 1$ and $\beta = 0$ indicating plausible models with maximal and minimal effects of hunting on survival, respectively. S_0 and K_t are each defined as applying when the other mortality source is not operating. As such, they are referred to as *net rates* in the literature of competing mortality risks (*e.g.* Berkson & Elveback 1960; Chiang 1968; see below). S_0 is not defined as time-specific (it is not subscripted by t), for consistency with historical development, but time-specificity is certainly possible conceptually.

Because S_0 and K_t are net rates, they cannot usually be estimated directly. Instead, without extra information about the timing of the different mortality sources, we are usually restricted to estimation of so-called 'crude' rates (*sensu* Chiang 1968). Specifically, a crude, source-specific mortality rate is the probability of dying from that source in the presence of all other mortality sources. In the case of modelling and inference about duck populations, K_t' is defined as the crude hunting mortality rate, or the probability that a bird alive at the beginning of the hunting season in year t would die from hunting causes during the hunting season of year t in the presence of non-hunting mortality that occurs during this period. Even K_t' cannot typically be estimated directly, but instead requires information from multiple sources. Ring recovery data are the common source of information about hunting mortality, and corresponding models permit direct estimation of ring recovery rates, f_t, the probability that a ringed bird alive at the beginning of the hunting season of year t is shot and retrieved by a hunter during the hunting season of year t and its ring correctly reported (see Brownie *et al.* 1985; Williams *et al.* 2002). Define c_t as the probability that a bird shot by a hunter during the hunting season of year t is retrieved by the hunter (1 – c_t denoting 'crippling loss'), and λ_t as the probability that a retrieved bird is reported. Then:

$$f_t = K_t' c_t \lambda_t \, . \tag{12}$$

If probabilities associated with ring reporting and retrieval are constant over time, then K_t' is related to f_t by a proportionality constant, making f_t a reasonable index of K_t' (see Anderson & Burnham 1976; Burnham & Anderson 1984; Burnham *et al.* 1984). And because non-hunting mortality during the hunting season is often thought to be small relative to hunting mortality, K_t', and thus f_t, are thought to be reasonable indices to K_t for the common situation (for North American waterfowl) of ringing occurring just before the hunting season.

Additive mortality hypothesis

Anderson & Burnham (1976) used equation (11) to define two endpoint hypotheses designed to bracket the possible relationships between total survival and hunting mortality. They used the term "additive" for the situation where $\beta = 1$, corresponding to a model in which hunting and non-hunting mortality sources are viewed as independent competing risks (Berkson & Elveback 1960; Chiang 1968). The term "additive" is applicable, as the instantaneous risks associated with the two mortality sources are added in order to obtain the total (both sources) probability of dying during an interval in which both sources apply. This additive mortality model is commonly used in fisheries management (Beverton & Holt 1957; Ricker 1958; Hilborn & Walters 1992) and is intuitively reasonable.

Although equation (11) applies to net rates of hunting and non-hunting mortality, regardless of their temporal patterns of occurrence, the intuition underlying this expression is perhaps most apparent when the two mortality sources are completely separated in time. So assume that only hunting mortality occurs during the hunting season and that all non-hunting mortality is restricted to the period following the hunting season. Then, equation (11) simply states that the probability of surviving the year is the product of first surviving hunting mortality during the hunting season and then surviving non-hunting mortality sources during the rest of the year. Because survival is a multiplicative process in time, with the survival probability for one period being applied to the survivors of the previous period, equation (11) should correspond to intuition. North American waterfowl management was based on the additive mortality hypothesis prior to 1976 (see Geis *et al.* 1969; Nichols 2000). Finally, note that equation (11) specifies a linear decrease in total annual survival, S_t, as net hunting mortality, K_t, increases (Anderson & Burnham 1976; Nichols *et al.* 1984; Fig. 5a).

Compensatory mortality hypothesis

Anderson & Burnham (1976) used equation (11) to specify a compensatory mortality hypothesis, under which $\beta = 0$ for some range of values of K_t, specifically for $K_t \leq C$ where C is a threshold subject to the inequality, $C \leq 1 - S_0$. So $S_t = S_0$ for $K_t \leq C$, that is changes in kill rate below the threshold induce no variation in total survival, which remains equal to net survival from non-hunting sources only. Because of this complete lack of influence of hunting mortality on total survival, at least for a range of hunting mortality rates, this basic model is sometimes referred to as depicting "complete compensation" (Conroy & Krementz 1990; Fig. 5b.). Kill rates greater than the threshold necessarily result in declines in total annual survival (linear decline under Anderson & Burnham 1976).

Conroy & Krementz (1990) noted that the diversity of life history characteristics among waterfowl (*e.g.* with respect to fast-slow and *r*–*K* variation) should lead to predictions about the degree to which particular species would be expected to exhibit more additive *versus* more compensatory mortality. Species with relatively "slow" life histories have higher survival rates and are expected to exhibit less ability to compensate for hunting losses than species with faster life histories characterised by much lower survival rates. At a minimum, total annual survival rates and net survival rates from non-hunting sources impose a constraint on the maximum value of a compensation threshold, $C \leq 1 - S_0$. Conroy & Krementz (1990) thus noted that a variety of hypotheses about hunting-survival relationships exists between the two endpoint hypotheses of additivity and complete compensation. They referred to these hypotheses as "partial compensation" and noted that they are characterised by $0 < \beta < 1$ in equation (11) below some threshold C (Fig. 5c).

Possible mechanisms for compensation. The family of hypotheses defined by equation (11) thus covers the full range of possible relationships between hunting mortality and total survival, ranging from complete additivity, to partial compensation to complete compensation (Fig. 5). However, a cost of this flexibility is that the model is phenomenological, in the sense that it provides no hint of plausible mechanisms that might underlie most of the possible hypotheses. Additivity, with $\beta = 1$, is consistent with intuition about how different mortality sources might interact. An individual can only die of one source and each death translates to fewer survivors at the end of any time period (*e.g.* 1 year). However, hypotheses reflecting some degree of compensation, $\beta < 1$, are not

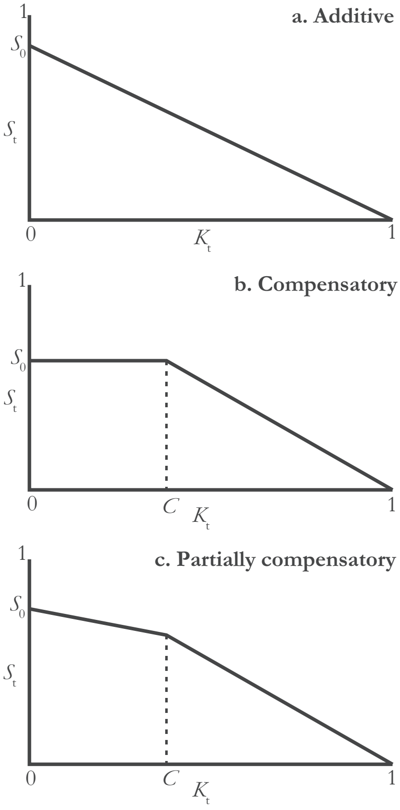

Figure 5. Additive (a), compensatory (b), and partially compensatory (c) mortality hypotheses. S_0 represents the net probability of surviving non-hunting mortality sources, which is also the theoretical survival rate in the absence of harvest. C is the threshold beyond which kill rate K affects S most strongly (where $C \leq 1 - S_0$). Adapted from Conroy & Krementz (1990).

necessarily intuitive and require some sort of underlying mechanism. Most of the discussions about compensatory mortality have involved one of two mechanisms, density-dependence and individual heterogeneity.

Density-dependence is the most frequently cited mechanistic hypothesis underlying compensatory mortality (Anderson & Burnham 1976; Nichols 1991). The usual explanation under density-dependence is that population size at the end of the hunting season is a determinant of subsequent survival during the portion of the year without hunting. In years where hunting mortality is large, abundance at the end of the hunting season is reduced, and each individual alive at this time has an increased probability of surviving the rest of the year. In years of low hunting mortality, abundance at the end of the hunting season is increased, and each individual has a lowered chance of surviving the rest of the year. Although we can fit equation (11) to data that derive from this mechanism, the actual mechanism is that the probability of surviving the hunting season is $1 - K_t$, and the magnitude of $S_{0,t}$ (the year-specific probability of surviving non-hunting mortality following the hunting season) now depends on abundance at the end of the hunting season, and thus on K_t.

Johnson *et al.* (1993) suggested a more mechanistic model designed to incorporate the above thinking about density-dependent non-hunting survival. The model consists of the following 2 expressions:

$$E(S_t) = S_{0,t}(1 - K_t), \tag{13}$$

and

$$S_{0,t} = \frac{e^{a+bN_t(1-K_t)}}{1 + e^{a+bN_t(1-K_t)}}, \tag{14}$$

where N_t is the population size at the beginning of the hunting season in year t, and a and b are parameters specifying the exact nature of the relationship between the probability of surviving non-hunting mortality and population size. Thus, equation (13) simply expresses the standard competing risks relationship that total survival is the product of the probability of surviving two risks, the probability of surviving hunting mortality (in the complete absence of non-hunting mortality) and the probability of surviving non-hunting mortality (in the complete absence of hunting mortality). Equation (14) then specifies that the probability of surviving non-hunting mortality risks is a function of the expected abundance at the end of the hunting season, N_t (1 – K_t). We note that strict application of this model with the above definitions assumes that only hunting mortality (no non-hunting mortality) occurs during the hunting season. However, if most of the mortality occurring during the hunting season results directly from hunting, then we can use K_t' as an index of K_t in the above expression. Of course there are other functional forms than the linear-logistic relationship of equation (14), and any such relationship would be more mechanistic than equation (11).

Characterisation of a model as phenomenological or mechanistic is of course subjective, and in reality these terms apply to regions along a continuum of mechanistic detail. For example, our use of population size at the end of the hunting season as the determinant of the probability of surviving the rest of the year represents a simplification (see Lebreton 2005). Density-dependence in ecological relationships typically involves some resource that is potentially in short supply, such that a more mechanistic depiction for equation (14) would be to substitute for N_t the number of animals *per unit of limiting resource* at the end of the hunting season. Despite substantive research on food resources during winter, clear linkages with subsequent survival implications are difficult to discern.

A second mechanism that can underlie compensatory responses (*i.e.* responses in which $\beta < 1$ in equation 11) involves heterogeneity among individual birds in underlying probabilities of surviving both hunting and non-hunting mortality sources (Johnson *et al.* 1986, 1988; Nichols 1991; Lebreton 2005; Sedinger & Herzog 2012; Lindberg *et al.* 2013). Arguments about the relevance of individual heterogeneity to animal population dynamics can be traced back at least as far as Errington (1943, 1967), who wrote about predation (one mortality source) and the fact that predated individuals would likely not have survived other sources had they survived predation. Writing about Muskrats *Ondatra zibethicus* that suffered predation, he wrote, "…they usually represented wastage, and, from the standpoint of the population biology of the species, it did not matter much what befell them" (Errington 1967: 155), and "the predation is centred upon….what is identifiable as the more biologically expendable parts of the population" (Errington 1967: 225). Errington's arguments about predation could be relevant to human hunting of waterfowl as well, if the segment of the population that experiences the higher hunting mortality rate also experiences the higher probability of dying from non-hunting mortality sources (Johnson *et al.* 1986, 1988; Lebreton 2005; Lindberg *et al.* 2013). With respect to the above modelling discussion of structured populations, hunting mortality is largest for the individuals of low quality with the lowest reproductive values.

For simplicity and ease of presentation assume that a population of ducks is characterised by heterogeneity of survival probabilities that can be approximated as a 2-point (finite) mixture (see "structure" section above, page 233), with the groups labelled as $g = 1, 2$. For ease of interpretation, also assume that the anniversary date each year is the beginning of the hunting season. Only hunting mortality occurs during the hunting season, and only non-hunting mortality occurs following the hunting season. This temporal partitioning of mortality sources is perhaps not a bad approximation for waterfowl and leads to views of seasonal hunting and non-hunting survival and mortality rates as net rates (rates that occur when only the focal mortality source is operating).

Define the following parameters:

π_t = probability, at the beginning of year t, that a randomly selected individual in the population is a member of group 1,

$1 - K_t^g$ = probability that a bird in group g ($g = 1$ or 2) survives exposure to hunting mortality during the hunting season of year t,

$1 - \bar{K}_t = \pi_t(1 - K_t^1) + (1 - \pi)(1 - K_t^2) =$ probability that a randomly selected member of the population survives exposure to hunting mortality during the hunting season of year t (mean net hunting survival), and

$S_{0,t}^g$ = probability that a bird in group g ($g = 1$ or 2) survives exposure to non-hunting mortality sources in year t, given that it is alive at the end of the hunting season.

The average probability of surviving non-hunting mortality sources for a randomly selected individual alive at the end of the hunting season is:

$$\bar{S}_{0,t} = S_{0,t}^1\left(\frac{\pi_t(1-K_t^1)}{\pi_t(1-K_t^1)+(1-\pi_t)(1-K_t^2)}\right) + S_{0,t}^2\left(\frac{(1-\pi_t)(1-K_t^2)}{\pi_t(1-K_t^1)+(1-\pi_t)(1-K_t^2)}\right). \quad (15)$$

Unlike the average probability of surviving hunting mortality, this population level average includes not only the initial probabilities of group membership, π_t and $1 - \pi_t$, but also the relative probabilities of surviving the hunting season. Thus, the terms in large parentheses reflect the expected proportions of the population at the end of the hunting season in each of the groups 1 and 2, respectively. The key concept in considering the influence of heterogeneity on population level effects of hunting is that the composition of the heterogeneous population changes (as reflected in these proportions) over time. If probabilities of surviving both hunting and non-hunting mortality are greater for one group than another, then this high survival group will increase in representation during the hunting season. This will lead to a greater average probability of surviving non-hunting sources than if both groups had experienced similar hunting mortality rates.

The population in the above example consists of two groups of birds, and each group is characterised by its own probabilities of surviving hunting and non-hunting mortality sources. If we assume additive mortality within each group of birds, then the probability that a bird in group *g* survives exposure to all mortality sources in year *t* can be written as:

$$S_t^g = S_{0,t}^g (1 - K_t^g) . \qquad (16)$$

Define $\overline{S}_t$ as the probability that an individual randomly selected from the population at the beginning of the year survives exposure to all mortality sources in year *t* (mean total survival at the population level). For the 2-group population considered above, we can write this total survival as:

$$\overline{S}_t = \pi_t S_{0,t}^1 (1 - K_t^1) + (1 - \pi_t) S_{0,t}^2 (1 - K_t^2) . \quad (17)$$

Consider two hypothetical groups of individuals in a heterogeneous population with corresponding probabilities of surviving hunting and non-hunting mortality sources given in Table 1. Individuals of group 1 experience higher probabilities of surviving both hunting and non-hunting mortality sources than individuals of group 2. Indeed annual probabilities of survival, computed using equation (17), are over twice as high for individuals of group 1, so the heterogeneity is substantial (Table 1). Average annual survival at the population level is computed using equation (16) as 0.53. The final row of Table 1 assumes a homogeneous population in which each individual is characterised by probabilities of surviving hunting and non-hunting mortality sources computed as weighted averages of the group-specific vital rates, with weights π_t and $1 - \pi_t$. The probability of surviving non-hunting mortality sources differs from the average for a heterogeneous population, because the homogeneous population value ignores the change in composition that occurs during the hunting season. The lower probability of surviving non-hunting mortality sources produces a lower annual survival rate for the homogeneous population (Table 1). These differences between heterogeneous and homogenous populations are attributable to the change in composition of the heterogeneous population (also see Vaupel & Yashin 1985; Johnson *et al.* 1986), and are consistent with the basic mechanism underlying Errington's (1967) ideas of the "doomed surplus".

The emphasis in this section has been on heterogeneity in survival probabilities, and the example in Table 1 suggests that substantial differences in survival among individuals do not necessarily produce large differences in total annual survival. Thus, both density-dependence and heterogeneous survival can mediate the effects of hunting on populations, but both processes are limited in their ability to compensate for hunting losses. Heterogeneous vital rates can also include reproduction. If the individuals that are better able to survive hunting and non-hunting mortality sources are also the better reproducers, then heterogeneity offers even greater potential for compensatory effects. Indeed, Lindberg *et al.* (2013) provided evidence that female Pacific Black Brant *Branta bernicla nigricans* exhibit heterogeneous survival and recruitment probabilities that lead to increased population growth rates, relative to growth of hypothetical homogeneous populations.

Evidence

Anderson & Burnham (1976) specified the two extreme hypotheses, additive mortality

Table 1. Survival rates in a heterogeneous population comprised of two groups of individuals with different survival rates. Mortality sources are restricted to seasons, with hunting mortality occurring first, followed by non-hunting mortality. Rates include net probabilities of surviving hunting ($1–K$) and non-hunting (S_0) mortality sources, as well as total annual survival (S). Rates are presented for individuals in group 1 and group 2. Average rates are based on the proportions of the populations in each group to which each rate applies. The homogeneous rates correspond to a population in which each individual experiences source-specific survival rates that are simple averages of those for the two groups.

Group (g)	**Proportion of population**	**$1–K$**	**S_0**	**S**
1	0.5	0.95	0.75	0.71
2	0.5	0.75	0.45	0.34
Average		0.85	0.62[a]	0.53
Homogenous		0.85	0.60	0.51

[a] Conditional on the expected population composition at the beginning of the season during which non-hunting mortality applies (computed using equation 15).

and compensatory mortality, and then analysed extensive ringing and recovery data for Mallard in North America to draw inferences about which hypothesis seemed to correspond most closely to these birds. They took advantage of the ring recovery models that had just been developed (Seber 1970; Brownie & Robson 1976; Brownie *et al.* 1978) to estimate annual survival rates and hunting mortality (kill) rates, and then to use these estimates with various analytic approaches for inference about hunting effects. They concluded that the Mallard data largely supported the compensatory mortality hypothesis, and that Mallard experienced hunting mortality rates that were typically below threshold levels.

A variety of improvements in analytic methods for testing these hypotheses followed the publication of Anderson & Burnham (1976), as did efforts to apply these various methods to other waterfowl species. These methods and results constitute a substantial literature that has been reviewed periodically (Nichols *et al.* 1984; USFWS 1988; Nichols 1991; Nichols & Johnson 1996). The most recent reviews (Nichols 1991; Nichols & Johnson 1996) show a mixed bag of results, with a number of studies providing evidence favouring the compensatory mortality hypothesis, some favouring the additive mortality hypothesis, and many providing equivocal results. This uncertainty led Nichols & Johnson (1996) to conclude that an adaptive approach to harvest management would be useful for the purposes of both managing harvest and learning about harvest effects (see the adaptive harvest management section, page 255 below).

Pöysä *et al.* (2004) reviewed previous studies on Mallard in North America, contrasting earlier work with the more recent efforts by Smith & Reynolds (1992, also see Sedinger & Rexstad 1994; Smith & Reynolds 1994). Based primarily on the Smith & Reynolds (1992) inferences from a more recent period (1979–1989), Pöysä *et al.* (2004) suggested that Mallard populations may have experienced a change in response to harvest over time, where hunting effects became additive, at least to some degree. Sedinger & Herzog (2012) argued that the conclusions of Pöysä *et al.* (2004) were unwarranted, but Pöysä *et al.* (2013) noted that despite some relevant points, the criticisms of Sedinger & Herzog (2012) did not cause them to change their conclusions.

Studies of compensatory *versus* additive mortality appearing after the review by Nichols & Johnson (1996) include four papers on ducks and several papers on goose species. The life history differences between ducks and geese (see above) lead to the observation that geese tend to have higher annual survival probabilities than ducks, and thus less potential to compensate for hunting losses. This observation leads to the expectation that many goose species will exhibit additive mortality, whereas ducks are more likely to exhibit possible compensatory mechanisms. Francis *et al.* (1998) analysed ringing and recovery data for American Black Duck *Anas rubripes* over three groupings of years characterised by increasingly restrictive hunting regulations. They found evidence of increases in survival rates, some consistent with the additive mortality hypothesis and some smaller than expected under this hypothesis (Francis *et al.* 1998). Conroy *et al.* (2002) developed various models to assess habitat and density-dependent effects on Black Duck survival. Model weights indicated support for models that reflected the additive mortality hypothesis. Rice *et al.* (2010) found no evidence that Pintail survival rates varied among groups of years characterised by different hunting regulations, but concluded that serious evaluation of effects of hunting was beyond their scope of investigation. Peron *et al.* (2012) developed an integrated population model for Redhead that used ringing and recovery data as well as information about abundance from the Waterfowl Breeding Population and Habitat Survey and about harvest age and sex ratios from the USFWS Harvest Survey. They found no evidence that Redhead survival varied in response to either daily bag limit or recovery rate, providing some support for the compensatory mortality hypothesis.

Alisauskas *et al.* (2011) conducted an extensive analysis of Lesser Snow Goose *Chen caerulescens caerulescens* population responses to increased harvest associated with special conservation measures designed to reduce abundances. They found some evidence of decreased annual survival rates associated with the additional harvest pressure for southern nesting populations, but no such evidence from the much larger northern population segments. However, Alisauskas *et al.* (2011) estimated much smaller increases in harvest rates associated with the conservation measures than had been hoped. An analysis of the southern La Pérouse Bay population of Lesser Snow Geese led Koons *et al.* (2014b) to conclude that young females exhibited evidence of compensation for an early time period, but evidence favoured additivity for young females in later years and adult females for the entire period of study. Two analyses of ringing and recovery data from G. Gauthier's long-term study of Greater Snow geese *Chen caerulescens atlantica* have focussed on effects of hunting on survival. Gauthier *et al.* (2001) provided evidence of additivity for the decade preceding a spring conservation harvest designed to reduce abundance. Calvert & Gauthier (2005) analysed ring recovery data for the initial years of the spring conservation harvest and found evidence of decreased survival (consistent with additive mortality) for adult Greater Snow Geese but not juveniles. Iverson *et al.* (2014) analysed ring recovery data for a population of Canada Geese in Ontario. Their analysis stratified individuals by reproductive status, and they found evidence of additivity for breeding adults, but not for non-reproductive birds. Sedinger *et al.* (2007) investigated variation in survival and recovery rates of Black Brant over the period 1950–2003 and found evidence of a decrease in recovery rate estimates over time, from early to more recent decades. These decreases in recovery rates were accompanied by an increase in annual survival rates, until recent decades when recovery rates became very small.

Results of studies summarised in previous reviews and the more recent work cited above provide mixed results. The majority of studies of effects of hunting on geese have provided at least some support for the additive mortality hypothesis, as predicted based on their typically slow life history and associated high survival rates. Studies of ducks have yielded period- and species-specific results, with some studies supporting the additive mortality hypothesis and others the partial and completely compensatory mortality hypotheses. Many of the papers reporting these analytic results ended with caveats and recommendations. The caveats virtually all involved the typically correlative nature of the efforts to study effects of hunting, and the acknowledgement that weak inferences are a likely result of this restriction. The recommendations were for either experimentation or adoption of an adaptive approach to harvest management as potential approaches to yielding stronger inferences. Adaptive approaches have been adopted for some species and do permit additional inferences about effects of hunting (see below).

Some methodological challenges

A variety of approaches exists for drawing inferences about effects of hunting. With the development of ring recovery models (Seber 1970; Brownie & Robson 1976; Brownie *et al.* 1978, 1985), waterfowl ringing programmes now permit estimation of ring recovery rates (indices to both crude and – for pre-season ringing – net hunting mortality rates, see page 236) and total annual survival rates. One straightforward approach to inference about hunting effects is to contrast recovery rates and annual survival rates for years of differing hunting regulations. If recovery rates indeed differ as predicted by the regulations changes, then an expectation under the additive mortality hypothesis is that annual survival rates are reduced in years with more liberal hunting regulations (*e.g.* larger daily bag limits or longer seasons).

Another seemingly straightforward approach is to correlate ring recovery rates and annual survival rates estimated from ring recovery data. However, as noted by Anderson & Burnham (1976) when these rate parameters are estimated from the same set of ring recovery data, the estimates are characterised by non-negligible sampling covariances. Because of these sampling covariances, simple correlation analyses using, for example, point estimates of time- or area-specific survival and recovery rates will yield inferences that confound true process covariation and sampling covariation, yielding correlation statistics that cannot be interpreted as pertaining strictly to the underlying mortality processes.

As a means of dealing with sampling variation, Burnham *et al.* (1984) proposed the direct fitting of the equation (11) (and a related power function model) to ring recovery data using a deterministic ultrastructural model. This approach to inference has been used in several waterfowl analyses (Barker *et al.* 1991; Smith & Reynolds 1992; Rexstad 1992). Otis & White (2004) developed a random effects approach to this kind of modelling by considering recovery rate as a random effect that covaries to some degree with annual survival because of possible effects of harvest on survival. This approach permits direct estimation of the process correlation (not confounded with sampling correlation) between recovery and survival rates, with a negative correlation expected under additivity and no correlation predicted under complete compensation. This approach was used for Canada Geese in Ontario by Iverson *et al.* (2014).

This basic approach of drawing inferences about effects of hunting by directly estimating the β of equation (11) or by estimating covariation of recovery and annual survival rates is appropriate for situations in which recovery rates are reasonable indices to net hunting mortality rates. We noted above that estimates of retrieval rates for hunter-killed birds and ring reporting rates are needed to translate ring recovery rates to crude hunting mortality rates. Retrieval rates are typically assumed to be approximately time-invariant, but these rates have received little study. Ring reporting rates have been studied, and if these vary over time and/or space, then they can and should be incorporated directly into inferences about hunting mortality rates. Reporting rate estimates can be incorporated into ring recovery analysis as constants (with or without sampling variation), or the raw data (*e.g.* recoveries from reward-ringed birds) used to estimate reporting rate can be incorporated into the analyses via joint likelihoods that include, for example, both standard and reward rings. We also noted that crude hunting mortality rates (rates obtained in the presence of other (non-hunting) mortality) are most useful for inferences about hunting when they are estimated from ringing that occurs just before the hunting season. When ringing occurs at other times of the year (*e.g.* post-season only), resulting data are not as useful for drawing inferences about hunting (*e.g.* see Nichols & Hines 1987) absent additional assumptions, as non-hunting survival becomes a potentially important source of variation in estimates of recovery rates and crude hunting mortality rates.

A variant (*e.g.* Sedinger *et al.* 2010) on this approach of investigating the correlation between ring recovery rates and annual survival substitutes Seber's (1970) reporting parameter, r_t, for ring recovery rate, f_t, where $f_t = r_t(1 - S_t)$. Use of a random effects approach, similar to that of Otis & White (2004), permits direct estimation of the process correlation absent any confounding with sampling variation. However, process correlations between S_t and r_t predicted under the compensatory and additive mortality hypotheses are not as straightforward as those expected for S_t and f_t. In analyses where ring recoveries are restricted to hunting recoveries, we can write Seber's reporting rate parameter as:

$$r_t = \left(\frac{K'_t}{1-S_t}\right) c_t \lambda_t = \left(\frac{K'_t}{K'_t + (1-S'_{0,t})}\right) c_t \lambda_t . \qquad (18)$$

The term in brackets is the probability that a bird that died during year t died as a result of hunting. The remaining terms are the probabilities of retrieval and ring reporting defined for equation (12). We have already indicated that rates of retrieval and ring reporting can either be estimated or else are frequently assumed to be constant over time. So the question for selecting f_t *versus* r_t is whether we prefer K'_t (see eqn. 12), or $K'_t/[K'_t + (1 - S'_{0,t})]$ (eqn. 18), as an index of net hunting mortality rate, K_t.

The difficulty in using r_t is that it is potentially influenced by non-hunting mortality in a manner that leads to a positive correlation with S_t. For example, if K'_t is constant, but $(1 - S'_{0,t})$ varies, then r_t will be larger when non-hunting mortality is smaller and total survival larger. Consider the numerical example of Table 2 in which we model additive mortality and again make the simplifying assumption that only hunting mortality occurs during the hunting season (thus $K'_t = K_t$) and only non-hunting mortality occurs following the hunting season (thus $1 - S'_{0,t} = (1 - K_t)(1 - S_{0,t})$; *i.e.* a bird must survive hunting mortality in order to be exposed to non-hunting mortality). We consider two years in Table 2, with constant rates of kill, retrieval, and ring reporting for both years, and differences only in the net probabilities of dying from non-hunting causes, $1 - S_{0,t}$. As a result of the variation in non-hunting mortality, both annual survival and the Seber (1970) reporting parameter are larger for the year of lower non-hunting mortality (year 2). So the process correlation between r_t and annual survival would be positive and possibly interpreted as evidence against additive mortality, whereas in reality additive mortality governed the survival process for both years. Note that there is no such indication of a positive correlation between ring recovery rate, f_t, and annual survival. In addition, note that Seber's (1970) reporting parameter, r_t, while incorporating what we have termed ring reporting rate, λ_t, is a very different quantity (eqn. 18) that attains very different values (Table 2).

Another basic approach to inference about additive and compensatory mortality is based on the relationship between net probabilities of experiencing hunting and non-hunting mortality, where "net"

Table 2. Numerical example illustrating the process correlation between Seber's (1970) reporting parameter, r_t, and total annual survival, S_t, under the additive mortality hypothesis. In the absence of variation in net hunting mortality, K_t, higher net probabilities of surviving non-hunting mortality, $S_{0,t}$, lead to higher r_t and S_t. Other definitions: c_t = probability that a bird shot in year t is retrieved, λ_t = probability that the ring of a bird shot and retrieved in the hunting season of year t is reported, f_t = ring recovery rate, $1 - S'_{0,t}$ = crude non-hunting mortality rate, and θ_t = probability that a bird which died during year t died as a result of hunting.

Year (t)	$K_t = K'_t$	c_t	λ_t	f_t^{a}	$S_{0,t}$	$1 - S'_{0,t}{}^{\text{b}}$	θ_t^{c}	S_t^{d}	r_t^{e}
1	0.200	0.800	0.750	0.120	0.600	0.320	0.385	0.480	0.231
2	0.200	0.800	0.750	0.120	0.800	0.160	0.556	0.640	0.333

[a] $f_t = K'_t c_t \lambda_t$; [b] $1 - S'_{0,t} = (1 - K_t)(1 - S_{0,t})$; [c] $\theta_t = \left(\dfrac{K'_t}{K'_t + (1 - S'_{0,t})} \right)$; [d] $S_t = (1 - K_t) S_{0,t}$;

[e] $r_t = \left(\dfrac{K'_t}{K'_t + (1 - S'_{0,t})} \right) c_t \lambda_t = \theta_t c_t \lambda_t$

indicates a mortality probability that would apply in the absence of any other mortality source (Chiang 1968). Both proposed mechanisms underlying compensatory mortality hypotheses suggest a change in one net mortality probability (non-hunting) as a function of variation in another net mortality probability (hunting). Density-dependence results in lower net non-hunting survival in years where hunting mortality is low, as many birds are alive at the end of the hunting season (other things being equal). Competition for resources is then hypothesised to result in lower net non-hunting survival of the survivors, than if hunting mortality had been larger. Under the heterogeneity hypothesis, the larger the hunting mortality rate the greater the change in composition of the heterogeneous population, leaving relatively more high survival group individuals, and thus greater average non-hunting survival. In summary, both density-dependence and heterogeneity lead to the prediction of a negative correlation between the net survival probabilities associated with the two mortality sources. Specifically, lower hunting mortality is associated with higher non-hunting mortality and *vice versa*.

If only hunting mortality occurs during the waterfowl hunting season and only non-hunting mortality occurs after the hunting season, then this temporal separation permits direct estimation of both net mortality rates via a ringing programme that includes ringing at two times of the year, the beginning and end of the hunting season. Inference based on a single ringing period each year is more difficult, however. Schaub & Pradel (2004) and Schaub & Lebreton (2004) used multistate models with recovery data based on annual ringing to estimate separate survival rates associated with two different mortality sources. However, it is important to recognise that these are "crude" rates (*sensu* Chiang 1968), as they are conditional on the deaths occurring as a result of the other mortality source. Above the crude hunting mortality rate, K'_t, is defined as the probability that a bird alive at the beginning of the hunting season in year t would die from hunting causes during the hunting season of year t in the presence of the non-hunting mortality that occurs during this period. Similarly, the crude mortality rate ($1 - S'_{0,t}$) could be defined as the probability that a bird alive at the beginning of the hunting season in year t would die from non-hunting causes throughout the year t in the presence of the hunting mortality that occurred earlier in the year.

There are two important difficulties to consider when using estimates of these crude rates, K'_t and $1 - S'_{0,t}$, to draw inferences about effects of hunting. The first difficulty is similar to that noted above for direct inferences about the relationship between annual survival and recovery rates, and involves the sampling covariance between time-specific estimates of these crude rates. These can be dealt with using either frequentist or Bayesian approaches (see Schaub & Lebreton 2004). The other difficulty is that these crude rates of hunting and non-hunting mortality are expected to exhibit negative process covariation for reasons that have nothing to do with changing net rates. This was noted by Schaub & Lebreton (2004) and Servanty *et al.* (2010) who refer to this component of process correlation as an "intrinsic bias" (Peron 2013 labelled it "competition bias"). To demonstrate this natural negative correlation between the two crude rates under the additive mortality hypothesis (*i.e.,* in the absence of any correlation between net rates), consider the following example of temporally separated hunting and non-hunting mortality. Assume that hunting mortality occurs first, and that this mortality is larger in year t_1 than in year t_2, $K'_{t1} = K_{t1} > K'_{t2} = K_{t2}$ (note that because of the timing of mortality, these are both crude and net rates). Assume that net non-hunting survival is the same in the 2 years; that is, survivors of the hunting season have equal chances of surviving non-hunting mortality in the two years, $S_{0,t1} = S_{0,t2}$. Thus there is no association between the net rates associated with non-hunting and hunting mortality in the two years. However, because of the greater hunting mortality in year 1, the crude non-hunting mortality rate will be smaller in year 1 than in year 2:

$$\begin{aligned}(1-S'_{0,t1}) &= (1-S_{0,t1})(1-K_{t1}) < (1-S'_{0,t2})\\ &= (1-S_{0,t2})(1-K_{t2}).\end{aligned}$$

Smaller numbers of birds are available to be exposed to non-hunting mortality sources in year 1; hence fewer die from these sources, despite equal net non-hunting rates in the 2 years. So the crude rates covary negatively, but this covariance is induced by variation in only one net rate and has nothing to do with the covariance between net rates that underlies compensatory mortality.

Although mortality sources were separated in time for our example, for ease of presentation, we note that the issue remains regardless of the timing of source-specific rates. Even when non-hunting and hunting mortality occur simultaneously, it is still true that more birds removed by one source (*e.g.* hunting) will leave fewer birds available to die of the competing source (non-hunting). Schaub & Lebreton (2004: 83) noted this problem when attempting to draw inferences about compensation or additivity using source-specific mortality data, but their important caveat does not seem to be appreciated by all others who have used this approach. Servanty *et al.* (2010) dealt with this issue by eliciting expert opinion about the timing and magnitude of non-hunting mortality, and incorporating these opinions using a Bayesian inference framework. In summary, we emphasise that attempts to use estimates of crude source-specific mortality rates (based on Schaub & Pradel 2004; Schaub & Lebreton 2004) to draw inferences about hunting effects require careful analysis and interpretation.

It is interesting that in work that is closely related in some ways to that of Servanty *et al.* (2010), but carried out 35 years previous, Brownie (1974) developed an approach to estimate the instantaneous risks (these translate directly into net mortality rates) associated with hunting and non-hunting using the extra information about the date of recovery of each hunting season ring recovery. She was able to estimate these risks directly, but had to assume that each was time-constant; the hunting risk throughout the hunting season and the non-hunting risk throughout the year. Even though she was able to separately estimate these annual risks without having to guess at their magnitude, she noted both the restrictive nature of her assumptions about temporal constancy of risks and the high sampling covariance between the estimates of risk, and abandoned this approach to inference about effects of hunting.

Finally, we note that radio-telemetry data are well suited to estimate net source-specific mortality rates (the rates from which strong inferences about compensation can be most readily obtained) directly. Time-specific deaths from sources other than a focal source can be immediately censored, providing direct inference about the net mortality rate of the focal source (Heisey & Fuller 1985; Heisey & Patterson 2006). Sandercock *et al.* (2011) provide a nice example of this approach to inference about compensation using a non-waterfowl species.

Reproduction

While assessment of the impact of harvest on waterfowl dynamics has generally (and intuitively) focussed on the direct relationship between harvest and survival (preceding section), harvest can potentially drive population dynamics in other ways, through the indirect influence of removal of individuals on other components of fitness. In this and the following section, we briefly consider the effects of harvest on components of reproduction, and on migration and movements.

Harvest can potentially influence reproduction in several ways. First, and perhaps most obviously, harvest clearly removes both the immediate and future (residual) contributions of a harvested individual to population growth. However, the typical accounting of the reproductive value of an individual, reflecting current and future reproductive contributions lost to harvest (*sensu* MacArthur 1960), assumes that such individual contributions to population growth represent independent events (*i.e.* that removal of one individual does not change the reproductive value of any other individual). However, in many cases per capita reproduction is influenced by the number (abundance or density) and structure (age, sex, spatial) of conspecifics. Density-dependence in population growth has been demonstrated at large spatial and temporal scales (Viljugrein *et al.* 2005; Sæther *et al.* 2008; Murray *et al.* 2010), and for many species of waterfowl (especially shorter lived ducks), variation in reproductive output is a dominant driver of annual population dynamics. Thus, it is reasonable to assume that any activity which reduces "density" (*e.g.* harvest) has the potential to increase population growth, by increasing reproductive productivity.

However, this conclusion is arguably overly simplistic, in at least a couple of respects. First, as noted by Lebreton (2009; also see above), estimates of density or population size are only a proxy for what affects demographic performance – a correlation between density or population size and reproductive performance is phenomenological, and does not generally indicate the important mechanisms underlying the observed relationship. This increases the uncertainty in projecting the impacts of harvest on population production, which is an important factor in decisions involving annual harvest regulations. For example, a reduction in total number of breeding individuals may not necessarily result in increased production at the population level, if the harvested individuals are lower quality birds which do not contribute significantly to annual production. Uncertainty about the functional form relating production to changes in abundance or density can be particularly important (Kokko 2001; Runge & Johnson 2002). Similarly, the influence of breeding population size on various components of post-laying fitness (*i.e.* events that might occur following the primary production of the clutch) may be more difficult to predict. For example, increased density of nesting birds may increase nest survival (Ringleman *et al.* 2014), but might lead to increased competition among juveniles for limiting resources, leading to reduced juvenile growth and survival (Cooch *et al.* 1991; Sedinger *et al.* 1995). It is probably true that for many species, the impact of population abundance (density) on both pre- and post-laying components of reproductive fitness will reflect a complex interaction of both frequency- and density-dependent effects, strongly influenced by various environmental effects which can significantly modify the relationships (Lebreton 2009).

Second, harvest not only has the potential to change the size of the population, but its structure (age, sex, spatial, heterogeneity) as well. Any harvest which changes the structure of a population will influence reproductive output, if those structural elements themselves influence one or more components of reproductive fitness, independently or in addition to potential density-dependent effects. For example, for species with polygynous mating systems, differential harvest of males and females might result in a skew to the sex-ratio in the breeding population, which could potentially influence the probability of any individual female laying a clutch, or the probability of that clutch surviving to fledging (in species where males and females play different roles in nest guarding and brood rearing), or both. Or, for species where breeding propensity may be based on relative proportions of individuals of different age or breeding experience at the start of breeding, differences in harvest vulnerability between younger and older birds could potentially be strong drivers for annual variation in the proportion of individuals breeding, which in turn would have a strong impact on population production. Changes to the structure of the population by harvest are not unexpected, since harvest is generally not random with respect to individual contributions to population growth. This non-randomness can be intentional (say, for example, due to a male only season or greater bag limit for males than females, or a region- or season-specific regulatory programme which allows for different harvest as a function of location and time of year), or an artefact of the interaction of non-specific (*i.e.* presumed random) harvest with structural differences in susceptibility to harvest. Such differences could reflect differences in vulnerability due to heterogeneity in individual reproductive performance (*e.g.* as a function of differences in timing of breeding, whether an individual bred at all that year, the timing and pattern of migration, number of offspring produced, or physiological condition following breeding).

Evidence

Much of the preceding is couched in terms of "potential impacts" of harvest on reproductive output, at either the individual or population level. In general, there seems to us to be a lack of consideration of the processes underlying the relationship between harvest and reproduction in waterfowl, beyond the obvious and logically trivial observation that a harvested individual has no future reproductive potential. Even seemingly simple (yet quite important) relationships between (say) harvest vulnerability and reproductive output are poorly quantified. For example, despite the long-held belief amongst many goose biologists that adults with young will have different vulnerability to harvest than adults without young, there are few rigorous attempts to quantify this relationship.

The relative paucity of empirical studies to date on the role of harvest on reproduction likely reflects several factors. First, there has been a general tendency to focus on impacts of harvest on survival, since: (i) the relationship of harvest and survival is potentially (and presumed to be) more accessible to management action, and (ii) the impacts of survival on overall population growth are often higher than possible impacts on reproduction, and thus are arguably more important to quantify. This is especially true for longer-lived species, where it has been shown repeatedly (to the point of redundancy, perhaps) that projected population growth is more sensitive to changes in adult survival than any other single demographic parameter (in fact, this result is a logical necessity for any species with a generation length greater than ~4–5 years; Lebreton & Clobert 1991; Caswell 2001; Niel & Lebreton 2005).

Second, evaluating the impacts of harvest on components of reproductive output (*e.g.* egg laying, nesting success, breeding proportions, recruitment) or population structure (*e.g.* sex ratio, spatial distribution) often requires intensive data from breeding ground studies, with adequate samples of marked, known-aged individuals for estimating some parameters. At present, there are a number of such studies involving breeding populations of geese, where high density nesting and strong natal philopatry lend themselves to collection of extensive, detailed demographic data. For example, Sedinger & Nicolai (2011) and Lindberg *et al.* (2013) have provided compelling evidence from their long-term study of Pacific Black Brant that harvest has both direct and indirect impacts on reproduction. Several near-replicate studies of a number of different goose species have clearly shown the negative impacts of density on clutch size (Cooch *et al.* 1989; Sedinger *et al.* 1998) and post-hatch growth and survival and recruitment of goslings (Cooch *et al.* 1991; Sedinger *et al.* 1995, 1998; Lepage *et al.* 1999).

In contrast, there are relatively few comparable studies involving breeding ducks, where natal dispersal and difficulty in capturing and marking broods makes analysis of variation of many reproductive parameters much more difficult. Exceptions to this general difficulty in studying nesting ducks are provided by cavity-nesting species, which can attain high nesting densities and exhibit high philopatry relative to most ground-nesting ducks. In Wood Ducks *Aix sponsa*, for example, high nesting densities have been associated with reductions in reproductive parameters such as breeding probability, nesting and hatching success, as well as with increased nest abandonment (Haramis & Thompson 1985; review in Nichols & Johnson 1990). With this exception of cavity-nesters, most of the empirical tests of the effect of density on components of reproductive rate for ducks relate to nest survival (*e.g.* Prop & Quinn 2003; Ringelman *et al.* 2014 and references therein). However, large-scale aggregate measures of reproductive rate (*e.g.* age ratios in autumn) have been related to population size and density in prairie-nesting Mallard of North America, providing some evidence of negative density-dependence (see Anderson 1975; Brown *et al.* 1976; Kaminski & Gluesing 1987; Johnson *et al.* 1997; also see page 260).

Even when a relationship between harvest and one or more components of reproductive performance has been established, the larger consequences on the dynamics (and management) of the population have not generally been considered. For example, while there have been a number of studies of the role of mate loss on reproductive success for several waterfowl species (Cooke *et al.* 1981; Martin *et al.* 1985; Forslund & Larsson 1991; Manlove *et al.*1998; Lercel *et al.* 1999; Hario *et al.* 2002), to our knowledge, there has been no rigorous assessment of the role of sex-specific differences in harvest vulnerability on population dynamics in waterfowl, although such studies are quite common for other taxa (see Milner *et al.* 2007). Similarly, a number of studies have suggested that lower quality individuals (based on various criteria, such as body condition) are likely more vulnerable to harvest (Hepp *et al.* 1986; Dufour *et al.* 1993; Heitmeyer *et al.* 1993; Pace & Afton 1999). Such non-random selection clearly has the potential to alter the structure and production of the breeding population. However, there has been little consideration of such selective harvesting and resulting changes in population structure on overall dynamics and management – the recent paper by Lindberg *et al.* (2013) is an important exception.

Migration/movement

Rates of movement are often ignored in discussions of population dynamics, yet they are important vital rates that bring about changes in population size at various scales. As with the other components of their population dynamics, there is convincing evidence that hunting can affect the movement rates of waterfowl.

Escape flights of waterfowl facing hunters are a common field observation and lead to local redistribution of the birds towards hunting-free refuges (Béchet *et al.* 2004). Ample demonstrations have been published of local increases in waterfowl numbers after reserve creation (Bellrose 1954; Madsen & Fox 1995; Fox & Madsen 1997; Madsen 1998a). Some authors demonstrated that such local movements were due to greater emigration rates from areas with more hunting pressure (*e.g.* hand-reared Mallard in Legagneux *et al.* 2009). However, protected areas may be attractive to birds not only because they are free from hunting, but also because they receive specific waterfowl-friendly habitat management. Several studies nevertheless have demonstrated that local redistribution of waterfowl towards protected areas was genuinely linked with hunting. For example, Madsen (1998b) established experimental reserves within a Danish fjord, which were moved from year to year. He documented concomitant changes in the annual distribution of hunted waterfowl species, which matched the movement of the reserves over time. Protected species conversely did not adjust their distribution to that of the reserves. Within a given year, Cox & Afton (1997) also recorded redistribution of female Northern Pintail depending on whether hunting was or was not occurring: the ducks increased their diurnal use of protected areas during two successive hunting periods, while this use decreased during the periods pre-hunting, post-hunting, and during the time between the two split hunting periods. It should be noted, though, that Link *et al.* (2011) did not obtain the same result in Mallard, which may indicate differential susceptibility of the different species to hunting disturbance and/or differences in habitat selection processes related with differential food availability.

Beyond such local scale effects, hunting has also been shown to affect waterfowl movement at the regional level (review in Madsen & Fox 1995). Ebbinge (1991) documented changes in the number of geese at the national scale in some countries after hunting was banned or, conversely, reintroduced in neighbouring countries. Madsen & Jepsen (1992) also reported that increased shooting pressure (together with changes in farming practices) led to an earlier departure of the Pink-footed Goose population from Denmark to the Netherlands during autumn migration. In ducks, Väänänen (2001) showed that Finnish *Anas* species move towards protected areas at the onset of the hunting season, and that their numbers also decline at the regional scale after this date, which may indicate that hunting precipitates fall migration in these species. This is consistent with Cox & Afton (2000) recording greater emigration rates of female Northern Pintail from Louisiana (largely towards other regions further north in the alluvial valley of the Mississippi River) during hunting periods than before, between or after these periods.

The potential effect of hunting on waterfowl movement rates is therefore clearly established. However, whether this later translates into lower survival or breeding output at the population level is not so clear. Gill & Sutherland (2000) and Gill *et al.* (2001) have already commented on the difficulty to predict the consequences of such disturbance at the population level based on observations of local responses of individuals (either through change in local time-activity budgets or in movement rates). Indeed, the local behaviour of individuals is dependent upon their respective abilities to respond locally (*i.e.* based on individual body condition, and/or the availability of alternative sites to the disturbed area), and the consequent effect at the population level may largely depend upon density-dependent processes.

To our knowledge, the only species in which the consequences of hunting for both individual movement and population dynamics have been demonstrated is the Greater Snow Goose. Spring hunting of this species at a migration area was introduced as a means to reduce the population and the problems caused to northern breeding habitats by these superabundant birds. The implementation of spring hunting changed the regional migration movements of these birds, with fewer unidirectional movements and more westward and reverse movements (Béchet *et al.* 2003). These changed movement patterns, a greater proportion of time spent alert and in flight, and greater use of less profitable habitats, resulted in poorer body condition of the geese after the initiation of the spring hunts (Béchet *et al.* 2004). Lower breeding output was in turn eventually recorded (Mainguy *et al.* 2002). Such an effect of hunting for population dynamics *via* changes in movement rates is also possible in other waterfowl species, but has yet to be demonstrated.

Adaptive harvest management

Overview

As noted in the above historical review, AHM was implemented by the USFWS for mid-continent Mallard in 1995 as a means of simultaneously managing in the face of uncertain harvest–population relationships and reducing this uncertainty. AHM programmes have now been implemented for other Mallard populations as well as for other waterfowl species (USFWS 2013). Here we briefly describe AHM components and the AHM process and then review what has been learned through its application to different Mallard populations.

"Adaptive management" has taken on many different meanings (Williams *et al.* 2009; Williams & Brown 2012), and our focus here will be on the passive process used by the USFWS in their various AHM programmes. This process requires some key elements: objectives, potential actions, model(s), a monitoring programme and a decision algorithm. Harvest management objectives are expressed as an objective function which typically is to maximise average annual harvest over a long time horizon. The time horizon places value on harvests from future waterfowl populations and thus serves to promote conservation. The potential actions are typically sets of regulations packages that specify season lengths and daily bag limits. At least one package is relatively restrictive (short seasons and small bag limits), at least one is relatively liberal (long seasons and large bags), and at least one package is moderate, where ideas about liberal and restrictive are typically population- and species-specific. An alternative approach to discrete regulations packages would be to specify a target harvest rate, treating this rate as a continuous control variable in the optimisation. However, because the regulations themselves are the actions selected by the USFWS, and because there is substantial uncertainty about the relationship between regulations and harvest rate (partial controllability), the USFWS has focussed on these discrete sets of regulations. In an effort to integrate the various potential actions available to manage waterfowl populations (including habitat management, for example), current deliberations are considering the modification of existing AHM programmes to incorporate additional objectives and additional kinds of actions (Runge *et al.* 2006; Osnas *et al.* 2014).

Models are required in order to predict population responses to management actions. Optimisation essentially entails a comparison of these predictions in order to select the action that is expected to do the best job of achieving management objectives. Models used in AHM are not simply models of waterfowl population processes, but are tailored to the specific purpose of predicting the consequences of actions to population change. Frequently, there is substantial uncertainty about population responses and associated models, and we refer to this as structural uncertainty. We attempt to incorporate this uncertainty into the models in one of two ways. The most commonly used approach to date has been the use of a discrete model set containing multiple models of system responses. Relative degrees of belief, or model weights, are associated with each model. These weights determine the influence of each model in the optimisation and are updated through time based on a comparison of model-based predictions and observations from monitoring programmes. The evolution of model weights over time reflects our learning. The other approach to dealing with model uncertainty is to employ a very general model and express the uncertainty as the variance of a key model parameter. In this case also, monitoring data are used to update estimates of the parameter and hopefully reduce its variance.

Monitoring programmes provide data that play several roles in the management process. They provide estimates of system state (*e.g.* population size) in order to make state-dependent decisions. State-dependence simply refers to the fact that we will typically take very different management actions when our focal population far exceeds a desired level as when our population is below the desired level. Estimates of system state are also used to see how well we are doing at meeting management objectives. Estimates of system state are essential to the process of learning, in providing an estimate of truth against which to compare our model-based predictions, thus providing a way to update model weights (discrete model set) or better estimate key model parameters that characterise our uncertainty.

Finally, some sort of decision algorithm must use these various components to determine an optimal action for each possible system state. Harvest management programmes are typically recurrent decision problems. For example, we usually make decisions about hunting regulations annually. Because optimal actions are state-specific and because an action taken at time t influences the state of the system, and thus the optimal decision, at time $t + 1$, the optimal decision at time t depends on projections of future system states and decisions. Dynamic optimisation algorithms are thus needed, with stochastic dynamic programming (Bellman 1957; Williams *et al.* 2002) being the method of choice for problems for which dimension is not too large. Although optimisation is recommended for decision making, we note that adaptive management can still be carried out, and learning can still occur, even when sub-optimal actions are taken.

Programmes of adaptive management typically require a deliberative or set-up phase during which the above components are all developed (*e.g.* Williams *et al.* 2007). At the first decision point, the optimisation algorithm is used to produce optimal state-dependent actions, based on the objectives, the available actions, and the model(s). These recommended actions are sometimes referred to as a policy matrix or decision matrix. The current state of the system is estimated via the monitoring programme and these estimates are used with the decision matrix to select the appropriate action for that decision point. The action is taken and drives the system to a new state, which is estimated by the monitoring programme. In the case of multiple models, the new estimate of system state is compared with the predictions of the different models, and the degrees of belief or weights associated with the models are modified using Bayes formula (see Williams *et al.* 2002). In the case of a single model characterised by uncertainty in one or more key parameters, these parameter estimates are updated with the new data. This completes the first step in the adaptive management process.

At this point, the process enters the iterative phase, and the next step is to consider the action to take at the next decision point. In the case of "passive" adaptive management (Nichols & Williams 2013), which has been used for most North American waterfowl management, the optimisation algorithm is run with the new model weights or updated parameter estimates. This produces a new decision matrix characterising the updated state of knowledge of system dynamics. This matrix is used with the estimate of current system state to select the optimal action for the upcoming decision point. This action is then taken, the system is driven to a new state identified by monitoring, information about that new state is used to update model weights and/or parameter estimates, and the process proceeds iteratively in this manner. In the case of waterfowl harvest, the decision points occur annually. After some experience (*e.g.* several years) with the process, there may be cause to reconsider some of its components. This has been referred to as double-loop learning (Williams *et al.* 2007) and entails moving back into the deliberative phase to revisit any of the process components, from objectives through models and monitoring. Indeed, this process of revisiting components is occurring now for some of the processes developed for adaptive harvest management of North American waterfowl, with special attention focussed on objectives and actions (*e.g.* incorporation of habitat management into decisions; Runge *et al.* 2006).

This basic process has been used to establish annual hunting regulations for mid-continent Mallard for nearly 19 years and for eastern Mallard for 14 years. As these are the longest-running programmes for North American waterfowl harvest management, they provide the best opportunities to learn about effects of harvest and to begin to discriminate among competing models of such effects. In the following two sections, we briefly review the competing models used in these two programmes and show the evolution of support (or lack of it) for these models.

Mid-continent and eastern Mallard

The mid-continent Mallard stock includes birds breeding in the traditional survey area of the waterfowl breeding population and habitat survey (WBPHS) strata 13–18, 20–50, and 75–77, plus birds observed in the states of Michigan, Minnesota, and Wisconsin (Fig. 6; USFWS 2013). Harvest policies derived for the Mississippi and Central Flyways are based on this population. The eastern Mallard stock includes birds breeding in the WBPHS strata 51–54 and 56 in the provinces of Ontario and Quebec plus birds breeding in the eastern states of Virginia northward into New Hampshire which are monitored through the Atlantic Flyway Breeding Waterfowl Survey. Harvest policies derived for the Atlantic Flyway are based on this population.

For each Mallard stock, a set of four models representing different combinations of recruitment and survival relationships are used to represent structural uncertainty and predict Mallard population responses to environmental changes and harvest regulations. For mid-continent Mallard, strong and weak density-dependent relationships are used to predict recruitment as a function of breeding population size and the number of Canadian ponds observed in the WBPHS (Fig. 7); while the eastern Mallard strong and weak recruitment models are based on a non-linear relationship that predicts annual recruitment as a function of breeding

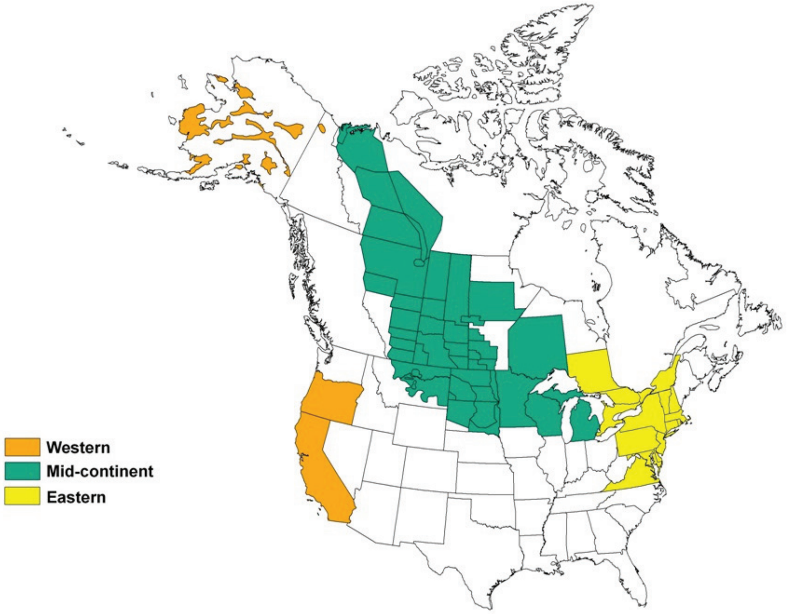

Figure 6. Distribution of eastern, mid-continent, and western Mallard stocks in North America, as described in the USFWS's adaptive harvest management programme.

population size only. Each model set also includes two survival sub-models to represent uncertainty in the relationship between harvest mortality and survival. These models are based on an ultra-structural formulation (see eqn. 11) that predicts annual survival as a function of the survival rate in the absence of harvest and the kill rate expected under a particular set of harvest regulations. Under the additive model, survival rates decline linearly with increasing harvest rates, while under the compensatory model, survival rates remain unchanged until a threshold harvest rate ($C \leq 1 - S_0$) has been exceeded and then decline linearly with increasing kill rates (see Fig. 7). Combining the recruitment and survival sub-models results in four models: additive hunting mortality and strong density-dependent recruitment (SaRs); compensatory hunting mortality and weak density-dependent recruitment (ScRw); additive hunting mortality and weak density-dependent recruitment (SaRw); and compensatory hunting mortality and strong density-dependent recruitment (ScRs). The mid-continent and eastern Mallard model sets were last updated in 2002 (Runge *et al.* 2002) and 2012 (USFWS 2013), respectively.

Under current AHM protocols, the relative belief we have in each model is quantified with an individual model weight. Because these weights sum to 1, they serve as individual measures of relative credibility. When AHM programmes were first implemented for these two populations, individual prior model weights were set equal (0.25), reflecting equal confidence in the

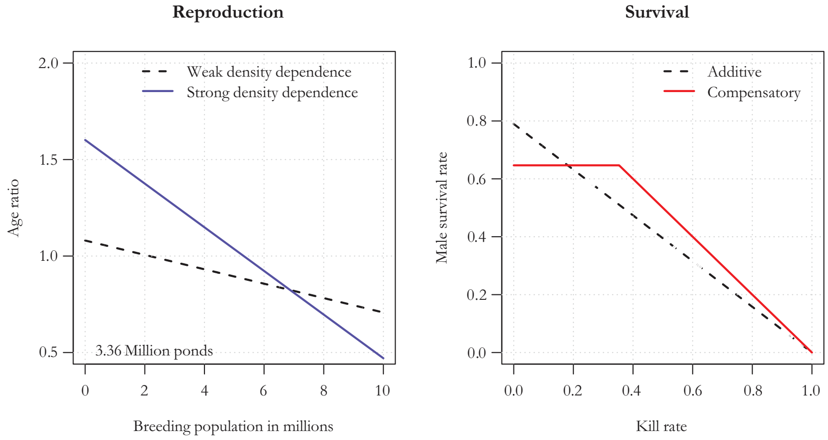

Figure 7. Reproductive and survival sub-models used to represent different relationships for recruitment and male survival in the mid-continent Mallard model set. Predicted levels of recruitment assume 3.36 million Canadian ponds.

ability of each model to predict Mallard population sizes. As observed population estimates were compared to individual model predictions, model weights and our relative beliefs in each model have been updated with Bayes theorem. For mid-continent Mallard, model weights remained essentially unchanged until 1999, when each model predicted a population decline in the face of a significant population increase (Fig. 8). Because the weak density-dependent model predictions were closer to the observed population estimates, they gained more weight and credibility. Since 1999, models SaRw and ScRw (weak density-dependent recruitment) have continued to gain credibility as weights for models SaRs and ScRs (strong density-dependent recruitment) have declined. For eastern Mallard, changes in model weights have been slower, with the additive mortality weak density-dependent model (SaRw) gradually accumulating more weight over time (Fig. 8).

The evolution of model weights over time resolves structural uncertainty and represents learning in adaptive management (Williams *et al.* 2002). Current model weights suggest strong evidence for weak density-dependent reproduction (96% and 68%) *versus* strong density-dependent reproduction (4% and 32%) in the mid-continent and eastern Mallard populations, respectively. For both the mid-continent and eastern Mallard stocks, model weights favor the additive mortality model (67% and 70%) compared to the compensatory mortality model (33% and 30%), suggesting support for the additive harvest mortality hypothesis. As the number of comparisons of model predictions to observed population estimates has increased over time, evidence has accumulated indicating that predictions from model SaRw are more reliable compared to other predictions from the model set.

However, it must be recognised that conclusions based on an interpretation of

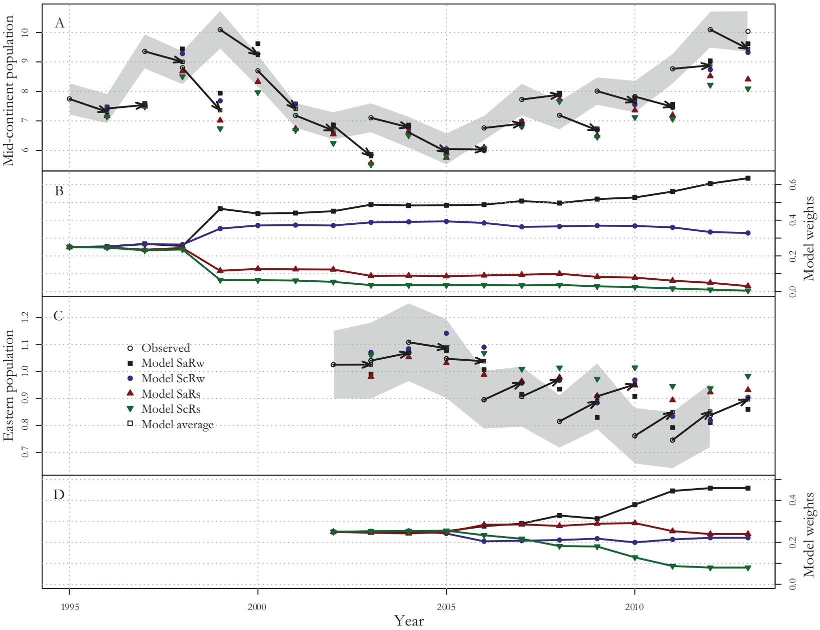

Figure 8. Panels A and C: population estimates of mid-continent and eastern Mallards (in millions) compared to predictions of each member of the mid-continent and eastern Mallard model set (SaRw = additive mortality and weakly density-dependent reproduction, ScRw = compensatory mortality and weakly density-dependent reproduction, SaRs = additive mortality and strongly density-dependent reproduction, ScRs = compensatory mortality and strongly density-dependent reproduction). The grey shading represents 95% confidence intervals for observed population estimates. For each model set, the arrow represents a weighted mean annual prediction. Panels B and D: annual changes in model weights for each member of the mid-continent and eastern Mallard model sets; weights were assumed to be equal in 1995 and 2002, respectively. For the eastern Mallard population, model weights were not updated in 2013 because breeding population estimates were not available.

relative credibility measures (model weights) are conditional on the set of hypotheses represented in the entire model set and that ecological interpretations are limited by the dependency of regulations on population status (Johnson *et al.* 2002; Sedinger & Herzog 2012). Recently, Sedinger & Herzog (2012) questioned whether current AHM model weights provide support for the additive mortality hypothesis, suggesting that this outcome may result from a spurious relationship between harvest and annual survival rates because density-dependent mortality is not explicitly considered in the AHM model set. They base part of their argument on results from Conn & Kendall (2004), who demonstrated through simulation, that the model weight updating procedures used in AHM may result in model weights that support the additive mortality hypothesis in cases where the true underlying dynamics were generated with a density-dependent, compensatory survival model. We note that the mid-continent Mallard model set and the prediction variance estimates that governed the model weight updating procedures simulated by Conn & Kendall (2004) were completely revamped during the 2002 revisions (for details see Runge *et al.* 2002). Simulation experiments using the current AHM protocols have verified that model weights converge on the correct model when the true generating model is included in the AHM model set (G.S. Boomer, unpubl. data).

We acknowledge that the true relationship between harvest and survival may not be represented well by the current model set and also note that model predictions may be consistent with observations without accurately representing the demographic relationships that determine population dynamics (Johnson *et al.* 2002). The current formulations of survival sub-models were included in the AHM model set to account for uncertainty in the relationship between harvest mortality and annual survival, specifying endpoints on a range of possible responses to harvest mortality. Certainly, an alternative harvest-survival model may perform better than each survival model in the current model set. The consideration of alternative beliefs in decision making is a hallmark of adaptive management, which provides a rigorous process to evaluate the ability of alternative models to predict the consequences of management actions. The current implementation of AHM provides an ideal framework to consider alternative models describing population responses to harvest management. We note that current efforts are underway to evaluate the sub-model performance of the eastern and mid-continent Mallard AHM protocols through the double-loop learning process. The continued successful application of adaptive harvest management requires that model sets are updated with the most recent information to ensure that key demographic relationships are properly represented and a full suite of population responses to management actions is considered.

Summary and conclusions

A defensible argument could be made that there has been and continues to be more interest (and pages published) related to harvest of biotic resources than perhaps any other subject in biology (studies related to disease dynamics being the only likely competitor). Our intent in this review was to provide a reasonably complete review of some of the current and historical interest in harvest, and harvest management, as pertains to waterfowl. However, beyond the usual difficulties of reviewing such a large literature, we were faced with the additional challenge presented by the fact that "ducks aren't geese, and geese aren't ducks…" (C.D. Ankney, pers. comm.). We have proposed that differences in life histories between most duck and goose species (reviewed briefly at the start of this paper) result in important differences in estimation and management of the impacts of harvest on their respective population dynamics.

Perhaps the most obvious and important difference between modelling goose and duck dynamics (with or without harvest) is the presence of significant "age structure" for goose species, and several sea ducks.

Specifically, for geese, we need to adequately account for significant age-specific differences in survival and fertility in the model. While the presence of greater degrees of age-structure for geese (and probably most sea ducks) is important, all species of waterfowl are likely "structured" to some degree, independent of possible age differences. For example, differences in survival or reproductive output as a function of location, or amongst individuals of differing "quality", are both forms of "structure" which are likely common to most waterfowl populations. We note that recent work by F.A. Johnson (pers. comm.) has extended this idea to multispecies management, where the structural component involves relative proportions of different species, and how one or more species can be managed when harvest might be in part a function of the structure and dynamics of the focal species. When populations are structured, the harvest required to achieve a particular management objective can be described as a vector (specifying the number or proportion of each structural class in the harvest), the elements of which are determined by: (i) the number of structural classes, and (ii) the reproductive value vector of individuals in each of those structural classes at the time of harvest. The inclusion of structure adds extra dimensions of uncertainty to harvest management. Most obvious is the need for estimation of an increased number of demographic rates and functional forms relating one or more vital rates to various intrinsic (population density, population structure, *etc.*) and extrinsic (*e.g.* climate variables) factors. While population size is often estimated annually, modelling and management of structured models also ideally requires an estimate of the structural composition of the population at each time step. In cases where harvest can be selective of individuals in different structural classes, an optimal harvest strategy may prescribe a structured harvest (*e.g.* so many big ones, so many small ones, *etc.*), with the actual structure of the harvest depending on harvest objectives.

However, for waterfowl species, we are usually limited in both our ability to characterise structure at the time of harvest (*i.e.* structure is often only partially observable), and to select the age or stage of the individuals that we harvest (*i.e.* harvest of specific classes of individuals is often only under partial control). More often than not, actual harvest is a function of an interaction of: (i) the harvest regulatory option(s), and (ii) the relative vulnerability to harvest of different classes of individuals in the population (young, old, male, female, *etc.*). In principle, adaptive harvest management approaches can be applied here, since they can explicitly account for such uncertainties. The larger technical challenge with applying AHM to structured populations is that the state of the population at the time of the annual harvest decision is only partially observable in many cases, and may need to be reconstructed in some form. Alternatively, you might accept that you are harvesting an unknown mixture, and that your expected returns will likely be reduced because of this uncertainty. To date, there is limited experience with application of AHM to such partially observable structured systems.

The differences between ducks and geese have important ramifications beyond the structure of population models. Of particular interest in the management context is that the management objectives can and occasionally do differ significantly between ducks and geese. For most ducks, the management objective can be stated simply as "we want enough birds in the population to keep it viable, in the presence of sustained mortality impacts from sport harvest". While this is generally also true for geese, for some populations of some goose species, there is the unique additional objective relating to limiting or reducing the size of the population. For example, light geese (primarily Lesser Snow Geese and Ross's Geese *Chen rossii*) in several parts of North America are demonstrably overabundant (Ankney 1996), and the current management objective for these populations is to reduce numbers to a point where habitat damage is mitigated, and (importantly) where normal harvest pressure can serve to keep the population in check (Batt 1997; Rockwell *et al.* 1997). What is interesting in this situation is that the "biocontrol" objective for light geese represents a clear paradigm shift for waterfowl management, in a couple of respects. First, it is entirely counter to the usual management perspective that 'more is better'. Among waterfowl managers, this view is probably heavily influenced by the perspective that there is "no such thing as too many ducks". The prevailing view is that because ducks are strongly limited by specific habitat requirements (*e.g.* ponds in breeding wetland areas), there is little potential for duck populations to exceed carrying capacity (which typically is one of several criteria by which a species might be considered as "over abundant"). Moreover, even if duck populations increased significantly relative to historical numbers, it is difficult for most biologists and managers to imagine duck populations causing major negative impacts to the environment (save, perhaps, for the increased likelihood of disease with increased density). In contrast, many goose species, primarily because of the significant differences they exhibit in foraging behaviour and bill morphology, and little evidence they have approached their overall carrying capacity, have been increasingly observed to have strongly negative impacts on their habitat (both winter and breeding), lead to detrimental collateral impacts on other wildlife species, and in some cases significant economic liability for agricultural crops (Abraham & Jefferies 1997; Batt 1997, 1998; Moser 2001).

Second, the "biocontrol" problem forces consideration of the underlying assumption that harvest, and therefore harvest management, is an efficient and effective tool to facilitate change in abundance. Traditionally, waterfowl management was premised on the belief that small changes in bag limits would lead to desired and detectable numerical responses in the target populations. However, despite special legislation passed to encourage very large increases in light goose harvest, there is strong empirical evidence to suggest that goose populations have not been controlled, and continue to increase (Alisauskas *et al.* 2011). There are at least two proposed explanations for the failure of harvest to significantly reduce goose numbers and limit further population growth. One is that the number of geese was simply too large for the current number of hunters to possibly control. While this is undoubtedly true to some degree, this problem is likely compounded by: 1) a functional response by geese becoming more wary and thus less vulnerable, or 2) some aspect of hunter behaviour, such as an attenuation in effort/hunter or general willingness to pursue Snow Geese after an initial interest for doing so during the beginning of the conservation order. Both a functional behavioural response by geese and changes in hunter behaviour were observed following implementation of liberalisations in Greater Snow Goose harvest regulations (Béchet *et al.* 2003; Calvert *et al.* 2007). Additional focus on understanding these aspects of partial controllability and hunter behaviour would be useful.

Regardless of whether the underlying mechanisms involve hunter behaviour or bird behaviour, the result for management is a need to modify model components relating hunting regulations to harvest rate. Rather than model harvest rate resulting from any fixed set of hunting regulations as characterised by a single probability distribution (Johnson *et al.* 1997; USFWS 2013), it will be necessary to consider a family of distributions associated with different population sizes. Above some threshold population size, average harvest rates for any fixed set of hunting regulations are hypothesised to decrease as a function of abundance. Incorporation of such density-dependent harvest rates into our management models highlights the fact that there are real and practical limits on the degree to which harvest can influence waterfowl population dynamics. Under an objective of population control, optimal management would attempt to maintain population size below the threshold at which population growth exceeds the capacity for control by harvest (see Hauser *et al.* 2007 for an example applied to the Atlantic Flyway population of Canada Geese). Thus, for fixed (frequently at maximally liberal levels for control objectives) hunting regulations, goose populations appear to respond in a *positive* density-dependent manner. This is quite different than typical duck management, where optimal strategies are conditioned by the expectation of some level of negative density-dependent feedback over the range of population sizes typically encountered.

Much of our presentation has focussed on "models" – specifically, population projection models which allow us to make predictions about the numerical trajectory of populations over time and space, and the degree to which those trajectories might be influenced by perturbation, natural or anthropogenic (in the context of this review, meaning "harvest"). The consideration of models focuses on two key points. Models represent canonical and (relatively) transparent representations about what we think we know concerning the factors which determine the dynamics of populations. Second, we can, and often do, use these models in applications. Here, we have focussed on models where dynamics are potentially impacted by harvest. These harvest models are used to project the consequences to waterfowl population dynamics of specified changes in rates of survival, fecundity, and in some cases movement. The major sources of uncertainty in waterfowl harvest management involve the translation of hunting regulations (the actions that we take) into various hunting mortality rates, and the subsequent translation of specific hunting mortality rates into changes in total rates of survival and fecundity.

With respect to the first source of uncertainty, hunting mortality rates are stochastically predictable for sets of hunting regulations with which we have experience. Uncertainty about translation of hunting mortality rates into population level effects is greater, but potentially reducible. The additive mortality hypothesis and the compensatory mortality hypothesis represent endpoints in which effects of hunting mortality on total survival are maximal and minimal, respectively. The additive mortality hypothesis corresponds to the idea of independent competing risks, whereas the compensatory mortality hypothesis is thought to require mechanisms such as density-dependent mortality or individual heterogeneity in survival probabilities.

A summary of evidence based on analyses for various waterfowl species leads to the general inference that the additive hunting mortality hypothesis represents a reasonable approximation to reality for most goose species. Results are quite varied for duck species to the point that generalisations are not really possible. It is not clear whether this inability to generalise is attributable to underlying processes varying across species, locations and even time periods, or instead to the difficulties of drawing inferences from observational studies. These latter difficulties led to our description of some commonly used techniques for such inferences, with warnings about possible pitfalls. Effects of changes in hunting mortality on reproductive output generally entail density-dependent responses, and there is evidence of negative density-dependent reproduction in a number of waterfowl species. Finally, there is also good evidence that hunting can influence waterfowl movement rates at spatial scales ranging from local to regional, but the population dynamic consequences of these movements are not well understood.

Traditionally, the use of such models (say, in harvest management) has been presented as something distinct from efforts to use models as a basis for discriminating among associated hypotheses. However, we submit that this dichotomy is a false one, and that use of models within a structured, adaptive management framework not only serves as a transparent, defensible mechanism to evaluate harvest objectives, but the process of harvest in turn provides a powerful experimental framework in which the various hypotheses about system dynamics inherent in the population models can be tested. Adaptive management was developed to aid decision making for recurrent decision problems characterised by potentially reducible structural uncertainty. The establishment of annual hunting regulations is certainly a recurrent decision problem, and the various hypotheses about population dynamic effects of hunting represent reducible structural uncertainty. A programme of adaptive harvest management (AHM) was established for mid-continent Mallard in 1995 and has been used to by the USFWS to develop hunting regulations for these birds since that time. AHM for eastern Mallard was initiated by the USFWS in 2000. AHM programmes have since been developed for other species and populations as well, but mid-continent and eastern Mallard provide our longest running examples. Evolution of model weights (measures of model credibility) shows that predictions of the models including weakly density-dependent reproduction and additive hunting mortality have performed best over the respective periods of operation of these two AHM programmes. In addition to this reduction in uncertainty (learning), AHM provides a basis for making decisions in the face of such uncertainty about processes governing population responses to management actions.

While there was probably no serious expectation that application of an AHM framework to harvest management of mid-continent Mallard would unequivocally come down as favouring one hypothesis or the other, results to date have formed the basis for much new thinking about not only the underlying mechanisms of compensation (*e.g.* the possible role of individual heterogeneity or alternative models to represent density-dependent survival), but also the policy elements of AHM. Perhaps one of the greatest benefits of AHM is that it provides a structured decision making approach that allows one to agree to a formal process while explicitly considering alternative beliefs (and disagreements) about management outcomes (Johnson & Case 2000). As the United States waterfowl harvest management community has entered the double-loop learning phase of AHM, much emphasis has been placed on the consideration of alternative harvest management objectives and possible linkages to habitat management programmes with formal connections to the human dimensions of waterfowl management (Runge *et al.* 2006; NAMWP 2014; Osnas *et al.* 2014). In addition to updating AHM model sets, the double-loop learning process of AHM has also offered an opportunity to think critically about large scale system change and how decision frameworks will need to be adjusted to cope with this new form of uncertainty (Nichols *et al.* 2011). As the interest in AHM has expanded, so has the variety of populations and systems for which it has been proposed (*e.g.* Hauser *et al.* 2007; Johnson *et al.* 2014). In developing these new applications, managers and waterfowl biologists are forced to identify important differences in the systems in question (*e.g.* system dimension and alternative harvest management objectives), and how well or directly experiences accumulated to date with (primarily) single species near-scalar duck models, apply to other systems, including (in particular) geese.

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