Drivers of waterfowl population dynamics: from teal to swans

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Abstract

Waterfowl are among the best studied and most extensively monitored species in the world. Given their global importance for sport and subsistence hunting, viewing and ecosystem functioning, great effort has been devoted since the middle part of the 20th century to understanding both the environmental and demographic mechanisms that influence waterfowl population and community dynamics. Here we use comparative approaches to summarise and contrast our understanding of waterfowl population dynamics across species as short-lived as the teal *Anas discors* and *A.crecca* to those such as the swans *Cygnus* sp. which have long life-spans. Specifically, we focus on population responses to vital rate perturbations across life history strategies, discuss bottom-up and top-down responses of waterfowl populations to global change, and summarise our current understanding of density dependence across waterfowl species. We close by identifying research needs and highlight ways to overcome the challenges of sustainably managing waterfowl populations in the 21st century.

Key words: climate change, demographic buffering and lability, density dependence, ducks, elasticity, environmental stochasticity, geese, population dynamics, swans.

Competition for and selection of available habitats throughout the annual cycle, trophic interactions and associated life history trade-offs can all affect individual fitness (Dawkins & Krebs 1979; Stearns 1992; Manly *et al.* 2002). Advances in our understanding of these topics were reviewed by the first three plenary sessions of the 6th North American Duck Symposium and Workshop, "Ecology and Conservation of North American Waterfowl," (ECNAW) in Memphis, Tennessee in January 2013. Ultimately, factors that have an impact on individual fitness can scale up to affect population dynamics via a change in mean fitness and also through the assembly of co-occurring species in a waterfowl community (Ricklefs 2008). The population remains the primary biological unit on which waterfowl management objectives are based (*e.g.* the North American Waterfowl Management Plan; Canadian Wildlife Service & U.S. Fish and Wildlife Service 2012), but a greater focus on the community of waterfowl species is starting to emerge (Péron & Koons 2013).

To set the stage for papers that review the roles of harvest (Cooch *et al.* 2014) as well as the combination of habitat and harvest (Osnas *et al.* 2014) when managing waterfowl populations, we begin by focusing on the basic demographic mechanisms governing waterfowl population dynamics, and how they interact with environmental conditions. We take a comparative approach by considering the full suite of waterfowl species that range from those as small as teal to those as large as swans, and assess the state of knowledge of waterfowl population ecology relative to relevant theories and to what is known for other animal taxa. First, we compare the functional response of population dynamics to life-cycle perturbations across waterfowl life history strategies. Second, we discuss how resistance to perturbation in one part of the life-cycle might in turn have a mechanistic connection to other stages in the life-cycle that are "more free" to vary over time and thereby can potentially make important contributions to observed changes in abundance. Third, we discuss areas that require additional research to provide a better understanding of the interplay between dynamic environmental conditions and demography in an era of global change that, fourth, can be augmented or tempered by density-regulating mechanisms.

Perturbation analyses across the slow–fast continuum in waterfowl

Waterfowl have evolved a diverse array of life histories: teal live a life almost as short as many passerines, whereas many swans and geese have annual survival rates of ~0.90 that can lead to average life spans of 10 years, and lifetimes in excess of 30 years for the longest-lived individuals. Although some waterfowl are quite long-lived, "penguins and albatrosses they are not" (*sensu* C.D. Ankney), as typical life spans in those groups are 20 years and some individuals live past 60 (U.S.G.S. Bird Banding Laboratory longevity records). Given their slow pace of life, long-lived species can afford to delay reproduction and invest in offspring "slowly" over their lifespan while balancing life history trade-offs. In contrast, in short-lived species a "fast" start to reproduction early in life is favoured to help ensure that individuals pass on genes to the next generation. This inter-specific pattern of life history strategies in birds and mammals has aptly become known as the "slow–fast continuum" (*sensu* Harvey & Zammuto 1985; Sæther 1988; Gaillard *et al.* 1989; Promislow & Harvey 1990; for an analogous life history theory in plants, see Grime 1977; Silvertown *et al.* 1992).

With greater longevity comes greater complexity in the age structure of a population. In turn, immediate population growth rates and long-term abundances are more sensitive to perturbations of the stable age distribution in long-lived species with slow life histories (*e.g.* geese, swans and eiders) than they are in short-lived species with fast life histories (*e.g.* teal; Koons *et al.* 2005, 2006a, 2007). These management-relevant effects of perturbed age structure on immediate and future abundance arise through demographic processes known as "transient dynamics" and "population momentum" (*cf.* Koons *et al.* 2006b). The importance of age structure in models for guiding harvest management is emphasised by Cooch *et al.* (2014) in this special issue (see also Hauser *et al.* 2006), but the general topics of age structure and its impact on transient dynamics and population momentum across waterfowl life history strategies are ripe areas for future research.

To the contrary, the impact of changes in vital rates (*i.e.* survival and reproductive success) on the long-term population growth rate is better studied for many waterfowl species. One popular metric for measuring the relative impact of vital rate perturbations is the "elasticity", which measures the effect of equal proportionate changes in vital rates on the focal metric of population dynamics (most often λ, the deterministic finite rate of growth; Caswell 2001). Elasticity analyses have been published for an array of waterfowl species including Mallard *Anas platyrhynchos* (Hoekman *et al.* 2002, 2006), Northern Pintail *Anas acuta* (Flint *et al.* 1998), Lesser Scaup *Aythya affinis* (Koons *et al.* 2006c), Greater Scaup *A. marila* (Flint *et al.* 2006), Long-tailed Duck *Clangula hyemalis* (Schamber *et al.* 2009), King Eider *Somateria spectabilis* (Bentzen & Powell 2012), Common Eider *Somateria mollissima* (Gilliland *et al.* 2009; Wilson *et al.* 2012), as well as Barnacle Goose *Branta leucopsis* (Tombre *et al.* 1998), Emperor Goose *Chen canagica* (Schmutz *et al.* 1997) and Snow Goose *Chen caerulescens* (Cooch *et al.* 2001; Aubry *et al.* 2010). We used studies like these and other published demographic data to construct simple matrix population models (following Oli & Zinner 2001) to compare the elasticities of λ to proportional changes in annual fertility (*i.e.* the rate of recruiting females to 1 year of age per adult female) and survival after the hatch year (AHY) across waterfowl life histories.

From dabbling ducks to pochard, shelduck, sea ducks, geese and swans, the elasticity of the population growth rate to changes in AHY survival increases with generation time (*i.e.* the average difference in age between parents and newborn offspring) whereas that to changes in fertility decreases with generation time (Fig. 1), a pattern common to all birds (Sæther & Bakke 2000; Stahl & Oli 2006). Given current data, only the Blue-winged Teal *Anas discors* has a higher elasticity for fertility than for AHY survival (Fig. 1). This implies that, all else being equal, the population growth rate will respond more readily to changes in AHY survival than it will to changes in fertility for the majority of waterfowl species that have moderate or long generation times. For species with very fast life histories like teal, however, the reverse is true.

Demographic buffering and lability in waterfowl life-cycles

Despite the greater sensitivity of λ to proportional changes in survival for

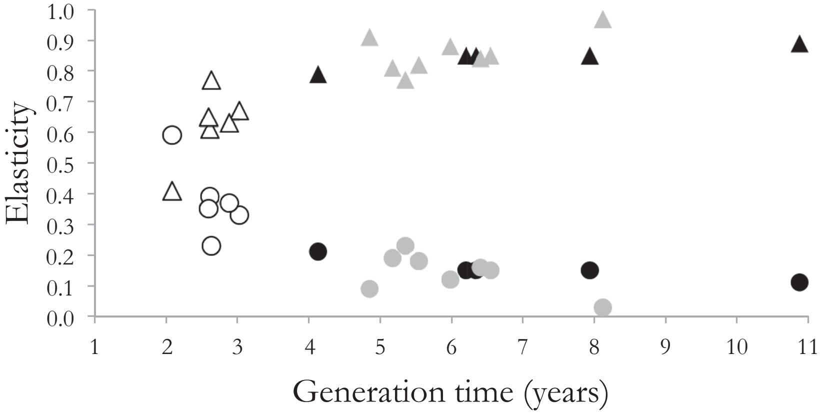

Figure 1. The elasticity of population growth rate (λ) to changes in annual fertility (circles) and adult survival (triangles) for 19 species of Nearctic and Palearctic ducks (white), shelduck and sea ducks (grey), and geese and swans (black), in relation to generation time (*i.e.* the average difference in age between parents and newborn offspring). On the far left are results for Blue-winged Teal and on the far right are results for Tundra Swan *Cygnus c. columbianus*. Elasticity results or demographic data used to conduct an elasticity analysis were extracted from: Patterson 1982; Rohwer 1985; Kennamer & Hepp 1987, 2000; Hepp *et al.* 1989; Hepp & Kennamer 1993; Flint *et al.* 1998; Cooch *et al.* 2001; Hoekman *et al.* 2002; Oli *et al.* 2002; Rohwer *et al.* 2002 and references therein; Flint *et al.* 2006; Grand *et al.* 2006 and references therein; Koons *et al.* 2006c; Gilliland *et al.* 2009.

many species, changes in the underlying components of fertility can still have management-relevant effects on λ. It is often the case that management actions cannot elicit the desired response in a vital rate (Baxter *et al.* 2006; Koons *et al.* 2014). When managers have difficulty influencing the vital rate(s) with the greatest elasticity, they might look to those that are most prone to being affected by changes in environmental conditions or management actions (*i.e.* the most labile). Actual changes in population abundance are not only a function of the vital rates with the greatest elasticities, but also density-dependent feedbacks (see section below) and the degree to which each vital rate changes over time (with fluctuations in age structure also contributing to changes in abundance; Davison *et al.* 2010). In fact, the contribution of each vital rate to past variation in population growth rate can be calculated analytically by using Life Table Response Experiments (LTRE), which comprise multiple approaches for best addressing the study hypothesis and design (Caswell 2001, 2010; see Cooch *et al.* 2001 for a waterfowl example). Over time, the contribution of a vital rate to past variation in population growth rate is proportional to the product of its squared elasticity and the square of its coefficient of process variation (when estimates are available, vital rate correlations should also be incorporated into calculations). Thus, a vital rate can make important contributions to changes in population growth by having a large elasticity, a large process variance, or both (eqn. 7 in Heppell *et al.* 1998).

In waterfowl, vital rate contributions to retrospective variation in λ have only been computed for Mallard (Hoekman *et al.* 2002; Amundson *et al.* 2012), King Eider (Bentzen & Powell 2012), Common Eider (Wilson *et al.* 2012), Barnacle Goose (Tombre *et al.* 1998) and Snow Goose (Cooch *et al.* 2001). A summary of these studies indicates that although adult survival may have the greatest elasticity, nesting success, pre-fledging survival and juvenile survival are often more labile to environmental conditions. As a result, variation in these fertility components can sometimes contribute more to observed variation in population dynamics than do changes in adult survival (see Gaillard *et al.* 1998 for similar results in ungulates). Yet, a larger contribution of fertility components to observed changes in λ does not necessarily imply that changing these vital rates will have a greater impact on population growth than would similar-sized changes in adult survival. Rather, fertility components could fluctuate enough over time to make important contributions to population dynamics (Caswell 2000). Managers might thus use LTRE and other variance decomposition methods (*e.g.* life-stage simulation analysis; Wisdom *et al.* 2000) as a platform for identifying the vital rates that can make important contributions to population growth through their natural lability to changing environmental conditions or management actions.

To gain a broader insight into which vital rates are most labile to environmental conditions across waterfowl life histories, it is necessary to understand the basic theory of population growth in stochastic environments. From first principles, the rate of growth for any population experiencing environmental stochasticity can be approximated as:

$$\ln \lambda_s \cong \ln \bar{\lambda} - \frac{\sigma^2}{2}, \qquad (1)$$

where $\ln \bar{\lambda}$ denotes the mean and σ^2 the variance of annual population growth rate (N_t/N_{t-1}) across environmental conditions on the log scale (Lewontin & Cohen 1969; Tuljapurkar 1982). Of key importance, increased variance in annual population growth rate decrements the long-term rate of growth in a stochastic environment ($\ln \lambda_s$).

Recognising this relationship, Gillespie (1977), and later Pfister (1998), noted that the vital rates with the greatest potential to affect mean fitness (*i.e.* $\ln \lambda_s$) should exhibit the least amount of temporal variance because organisms should presumably be selected to avoid fluctuations in vital rates that would have severe negative impacts. Over the long-term, natural selection should have favoured such life history properties; a concept that has become known as the Demographic Buffering hypothesis (DB; Gaillard *et al.* 2000; Boyce *et al.* 2006). There is general support for the DB hypothesis in plants and diverse animal species (*e.g.* Morris *et al.* 2008; Dalgleish *et al.* 2010; Rotella *et al.* 2012) including birds (Schmutz 2009). Avian species with high adult survival elasticities tend to exhibit less variation in adult survival over time than do species with low adult survival elasticities. In all comparative studies, however, empirical fits to DB predictions are not perfect; there is often a great deal of deviation from the predicted negative relationship between vital rate elasticities and temporal variation in vital rates (Jäkäläniemi *et al.* 2013). Among waterfowl, currently available data for temporal variation in adult survival do not support the DB hypothesis (Fig. 2).

Mixed support for the DB hypothesis could occur for a variety of reasons. For example, few studies are able to study the entire life-cycle of a population over a long enough period of time to attain proper estimates of temporal "process variation" in each vital rate (see Rotella *et al.* 2012 for an example of the benefits provided by such estimates). Unfortunately, ignoring the issue of vital rate variance decomposition in tests of the DB hypothesis will inevitably inflate type II errors (Morris & Doak 2002). In addition, rapid anthropogenic alterations to the environment might have exceeded the capacity of organisms to buffer or respond to environmental fluctuations (Schmutz 2009). At a fundamental level, the DB concept is also restricted and cannot always capture the full effects of environmental stochasticity on $\ln\lambda_s$. Optimising fitness in a stochastic world is a balancing act of increasing mean vital rates, which affects the first term on the right-hand side of eqn. 1, but also decreasing variance in vital rates, which minimises the negative effect of the second term. It has only recently been recognised that temporal variation in vital rates can have a positive impact on $\ln\lambda_s$ when the variation induces an increase in $\ln\bar{\lambda}$ that is sufficiently large to outweigh the negative effect of σ^2 (see eqn. 1; Drake 2005; Koons *et al.* 2009). This can occur

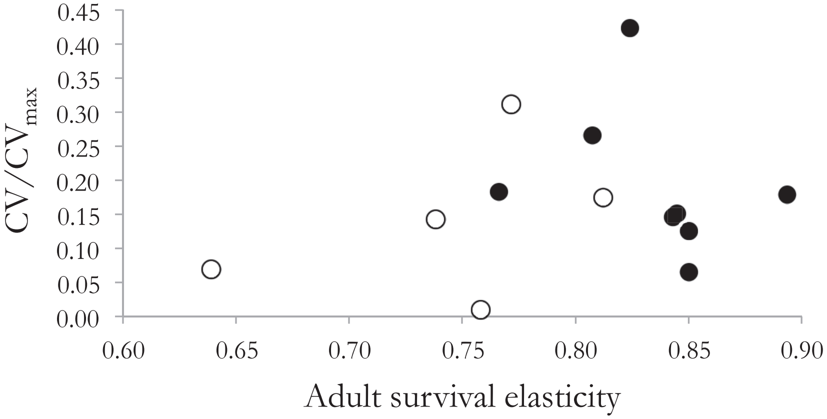

Figure 2. The relationship ($P > 0.10$, n.s.) between adult survival elasticities and the relative temporal "process variation" in adult survival across 13 waterfowl populations (white for ducks and black for geese; no sea duck data were available for these analyses). The coefficient of process variation (CV) was divided by the theoretically maximum possible value of CV for a given mean survival probability (see Morris & Doak 2004). Similar results were achieved using raw values of CV. The waterfowl data were extracted from Schmutz (2009) and references therein, as was the approach to developing matrix population models for the calculation of elasticities.

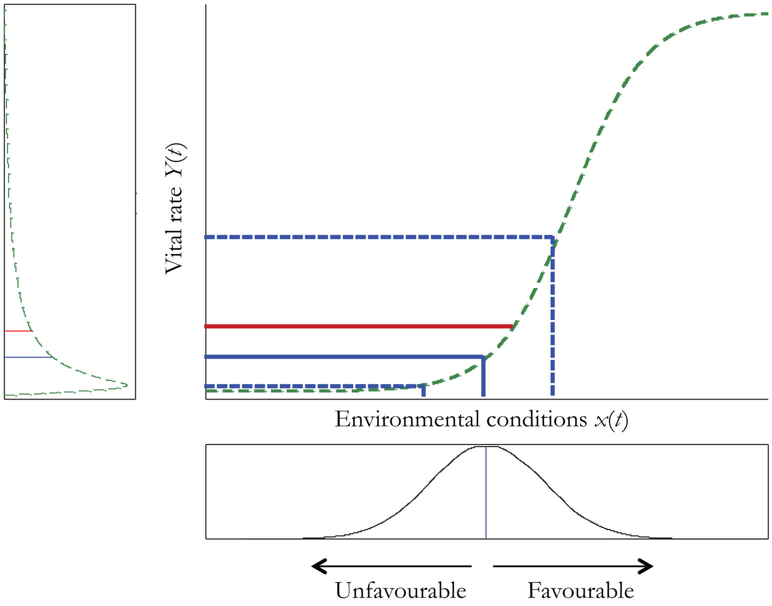

Figure 3. A hypothetical sigmoid relationship between an environmental variable (x) and any vital rate Y. The lower box illustrates the mean (blue bar) and temporal distribution of environmental conditions $x(t)$. The left box indicates the resulting temporal distribution of vital rate $Y(t)$. The solid blue bars in the main figure illustrate vital rate performance in the average environment. The dashed blue bars show vital rate performance 1 s.d. below and above the average environment. As conditions vary over time, favourable environments produce larger increases in vital rate performance than decreases experienced in equally unfavourable environments. In turn, this raises the mean of Y and the long-term stochastic growth rate (red lines). The Demographic Buffering hypothesis implicitly assumes a linear relationship between $x(t)$ and $Y(t)$, in which case variation in $x(t)$ has no effect on the mean of Y, only its statistical variance.

when a vital rate has a convex relationship with prevailing environmental conditions (Fig. 3). Although the effect of "variance" in the strictest sense will still be negative, variation across convex relationships with environmental variables can "skew" the distribution of a vital rate and increase its mean value (Fig. 3), thereby increasing $\ln\bar{\lambda}$ (the interested reader should see Rice *et al.* 2011 for a decomposition of $\ln\bar{\lambda}$ that is more complete than the commonly used approximation shown in eqn. 1).

For vital rates that are on average low, such as nest success (*i.e.* the proportion of clutches where at least one egg hatches) in many duck populations, or offspring survival in some goose and swan populations, the potential for convex relationships with niche axes is strong. If such relationships occur, enhanced environmental stochasticity could actually be beneficial because favourable conditions could induce booms in vital rates that enhance the long-term stochastic population growth rate (Koons *et al.* 2009;

Walker *et al.* 2013). Further research on DB and lability in waterfowl is nevertheless needed to provide a better understanding of how vital rates will respond to global change across species, and how such responses will affect population growth rates.

Demographic drivers in an era of global change

For waterfowl management to keep pace with climate, land-use and water-use changes in the 21st century, a greater depth of knowledge is needed of the mechanisms affecting demography and population dynamics. Habitat and predation continue to be central topics of waterfowl research and management (*e.g.* Duebbert & Kantrud 1974) but we must also prepare for changes in the dynamic interplay between abiotic conditions and trophic interactions. Some regions of the Nearctic and Palearctic are becoming warmer while others are not; some may receive more precipitation and others less (IPCC 2013). Many landscapes are being converted to produce more ethanol, wind or solar power (Northrup & Wittemyer 2013; Wright & Wimberly 2013), and greater human demands for land and water will continue to affect the amounts and quality of habitat available to wildlife (Fischer & Heilig 1997; Lemly *et al.* 2000; Pringle 2000). The aforementioned changes describe shifts in the "mean" environmental conditions that often come to mind when we speak of global change in the 21st century. Some outcomes of these changes are predictable; less water or breeding habitat would likely lead to fewer ducks (Reynolds *et al.* 2001; Stephens *et al.* 2005), whereas more corn planted for ethanol production could compound the ongoing problem of over-abundant goose populations (Ankney 1996; Abraham *et al.* 2005).

In addition to predicted changes in mean climatic conditions, increases in the variability of climate could also occur in many parts of the Nearctic and Palearctic (*e.g.* Wetherald 2009), including the prairie pothole region of North America (Johnson *et al.* 2010). This could imply greater extremity in climate from year to year; for instance, very dry years followed by heavy precipitation that leads to flooding, or balmy winters followed by bitter cold ones. Other than the direct effects of exposure, climate tends to affect waterfowl populations through changes in bottom-up food resources, top-down predation, and density-dependent interactions (Nudds 1992).

Trophic ecologists in Scandinavia have shown that the shape of a predator-prey functional response can determine fundamentally whether increased temporal variation in a resource has a positive or negative effect on the mean vital rates of a consumer (*e.g.* Henden *et al.* 2008). In other words, trophic interactions can dictate the relative advantages of DB *versus* lability in a population. In other systems, climate-driven pulses in primary productivity can result in counter-acting direct and time-lagged effects on primary consumers because of complex trophic interactions such as apparent competition (Schmidt & Ostfeld 2008). For example, in the prairie pothole region, Walker *et al.* (2013) found that duck nest success in year t was positively associated with pond density and primary productivity in the same year (t), but negatively related to these variables in previous years (t–1 and *t*–2). Findings like these could possibly be attributed to the positive numerical response of alternate prey to climate-induced change in primary productivity, which could swamp out generalist predators in the current year, but then lead to numerical responses in predator populations that later have a deleterious effect on waterfowl reproductive success (Ackerman 2002; Brook *et al.* 2008; Schmidt & Ostfeld 2008; Iles *et al.* 2013a; Walker *et al.* 2013).

Changing mean and variance of climatic conditions can also affect waterfowl populations through differential changes in phenology across trophic levels. For example, the match-mismatch hypothesis predicts that a consumer should try to "match" its life-cycle events with the timing of maximal resource availability or quality because failure to do so results in a "mismatch" between resource and consumer phenologies that reduces fitness (Visser & Both 2005). Research on the match-mismatch hypothesis in ducks is advancing (*e.g.* Drever & Clark 2007; Sjöberg et al. 2011), and species with less flexible nesting phenology (*e.g.* scaup and scoters; Gurney *et al.* 2011) might suffer more from climate-induced shifts in the timing of resource availability compared to those that are more flexible (*e.g.* Mallard; Drever *et al.* 2012).

Research on the match-mismatch hypothesis in geese indicates that warming of the Arctic has led to, on average, earlier greening of graminoid plants that can readily take advantage of early growing degree days (van der Jeugd *et al.* 2009; Doiron *et al.* 2013; Gauthier *et al.* 2013). Some arctic geese have, however, evolved to balance their timing of migration with photoperiod, plant phenology and resource availability along migration paths, as well as plant phenology and snow cover on the breeding grounds (Strong & Trost 1994; Gwinner 1996; Bauer *et al.* 2008, Tombre *et al.* 2008). Thus, they cannot always "match" their nesting phenology with the greening of graminoid forage on the breeding grounds (Gauthier *et al.* 2013). A year of late nesting relative to the phenology of graminoid greening can result in reduced food quality for goslings that in turn inhibits their growth, body condition and ultimately survival (Dickey *et al.* 2008; Aubry *et al.* 2013). However, the trend toward earlier greening is not consistent from year to year because the variability in growing degree days in spring seems to be getting larger. Although the trend toward earlier greening may force a mismatch between arctic geese and their preferred forage, stochasticity in the near-term will still provide some years where they can match their nesting to plant phenology (Aubry *et al.* 2013).

Climate-driven changes in phenology can also affect the intensity of top-down predation and even result in completely novel predator-prey interactions. For example, climate-driven declines in the extent and duration of sea ice each year have been linked to earlier onshore arrival of Polar Bears *Ursus maritimus* in many parts of the Arctic and reduced opportunities for the Polar Bears to hunt seals (Family: Phocidae and Otariidae; Stirling & Derocher 1993; Stirling & Parkinson 2006). This has resulted in a mismatch for Polar Bears with their preferred seal prey. Ironically, this now exposes Polar Bears to a novel overlap with the breeding seasons of many ground-nesting waterfowl populations (Rockwell & Gormezano 2009), from which they are readily consuming eggs and offspring (Madsen *et al.* 1998; Noel *et al.* 2005; Drent & Prop 2008; Smith *et al.* 2010; Iles *et al.* 2013b; Gormezano & Rockwell 2013; Iverson *et al.* 2014). Novel predator-prey interactions such as these have strong potential to affect waterfowl population dynamics (Rockwell *et al.* 2011). Climate change could thus affect waterfowl populations through changes in both bottom-up and top-down interactions. Yet the strength of these interactions, as well as those among conspecifics, may be moderated by population density and the ability of individual species to respond to the novel selection pressures induced by climate change.

Density dependence: the ever-elusive regulator of populations

Population density affects population dynamics through both intra- and inter-specific interactions. For example, density can influence competition for territories and mates, competition for and depletion of limited foods, rates of pathogen transmission, and functional responses of predators. Density can also act in positive ways. In arctic geese, for example, colonial nesting density and intermediate levels of grazing have both been shown to enhance vital rates (*e.g.* Raveling 1989; Hik & Jefferies 1990; Aubry *et al.* 2013). Both positive and negative density-dependent interactions scale up to affect vital rates in ways that shape the pace of population growth and, ultimately, negative density dependence at some point in the life-cycle places an upper bound on the capacity of a population to grow (Turchin 2003). Ever since Malthus (1798), density dependence has therefore been central to our way of thinking about population dynamics. Given its role in affecting population growth, harvest management has often been used to manipulate population density in an attempt to optimise long-term yield from populations (*e.g.* maximum sustainable yield theory; Walters 1986). On the other hand, habitat management attempts to manipulate the carrying capacity by providing more per capita resources, and thereby increasing the ceiling on abundance where reproductive success and mortality balance each other out (Smith *et al.* 1989). Only recently has waterfowl management begun a formal integration of these concepts, which are tied both to density dependence and to environmental change (Runge *et al.* 2006; Mattsson *et al.* 2012), a topic specifically addressed by Osnas *et al.* (2014) in this volume. For these reasons, and others, it is critical to improve our understanding of how density dependence operates over the annual life-cycle, and across the diverse array of waterfowl life histories (Gunnarsson *et al.* 2013).

Measuring the influence of density dependence on population dynamics in the wild, however, has been said to be "like a search for the holy grail" (Krebs 1995). Two demographic approaches have nevertheless been employed to make progress toward understanding density dependence: surveys of population abundance, and studies of life history traits (Lebreton & Gimenez 2013). Time series analyses of how surveyed abundance responds to levels of population abundance in previous years are *sensu stricto* phenomenological (Krebs 2002) but can, with care, be used to test for the presence of density dependence, measure its impact relative to environmental variables, and even examine the interactive effects of variation in population density and environmental variables on population dynamics (*e.g.* Stenseth *et al.* 2003; Rotella *et al.* 2009). The long-standing problem, however, has been the lack of independence between explanatory and response variables and the related issue of shared sampling variation (*i.e.* uncertainty in abundance) between the axes being analysed, both of which bias estimation towards greater strength (and presence) of density dependence than actually exists (Freckleton *et al.* 2006; Lebreton & Gimenez 2013). Unfortunately, many older published studies did not account for analytical problems that induce these false positives. The results of those studies should probably be disregarded and, where available data allow, the information should be re-analysed with modern methods to improve our understanding of density dependence. Modern state-space statistical models for time-series data can account for these issues (*e.g.* Knape & de Valpine 2012; Delean *et al.* 2013) and help make use of widely available monitoring data to gain insight into the influence of density dependence on waterfowl population dynamics over time (Murray *et al.* 2010), space (Viljugrein *et al.* 2005), and across life histories (Jamieson & Brooks 2004; Sæther *et al.* 2008; Murray *et al.* 2010).

The approach of studying the effects of population density on life history traits nicely avoids the issue of dependence between explanatory and response variables. That said, uncertainty in estimates of population abundance (the explanatory variable) can result in bias toward false absence of density dependence (McArdle 2003); a conservative outcome that is often more favoured in science than a false positive (Lebreton & Gimenez 2013). When conducted with explicit attention to biotic interactions, the life history trait approach can provide a deeper understanding of density dependence than can analyses of abundance time series (Krebs 2002). Such approaches have been used nicely in both observational and experimental waterfowl studies to elucidate the mechanistic effects of population density on fidelity and adult breeding probability (Sedinger *et al.* 2008), clutch size (Cooch *et al.* 1989; Sedinger *et al.* 1998), nesting success (Raveling 1989 for geese; Gunnarsson & Elmberg 2008; Ringleman *et al.* 2012 for ducks; see Gunnarsson *et al.* 2013 for a review), offspring growth (Lindholm *et al.* 1994; Schmutz & Laing 2002; Person *et al.* 2003), offspring survival (Williams *et al.* 1993; Nicolai & Sedinger 2012 for geese; Gunnarsson *et al.* 2006; Amundson *et al.* 2011 for ducks; see Gunnarsson *et al.* 2013 for review), subsequent post-fledging survival (*e.g.* Schmutz 1993; Sedinger & Chelgren 2007; Aubry *et al.* 2013) and even the effects of nutrient limitation during development on eventual adult body size (*e.g.* Cooch *et al.* 1991a,b; Sedinger *et al.* 1995; Loonen *et al.* 1997). Moreover, density dependence at one stage of the life-cycle (*e.g.* nesting) can affect population density and its impact later in the life-cycle (*e.g.* offspring rearing and then post-fledging) through a sequential cohort process (Elmberg *et al.* 2005).

Although its effects are complex, great progress has been made in recent years toward understanding the role of density dependence in waterfowl (Gunnarsson *et al.* 2013). Lack of long-term and experimental studies for many taxa and the aforementioned issues with estimation currently prevent us from being able to make robust conclusions about patterns in density dependence across waterfowl life histories. When resources are limited, density dependence can have strong effects on reproductive success of the most fecund (*e.g.* Mallard; Kaminski & Gluesing 1987) and even the most long-lived of waterfowl species (*e.g.* arctic geese and swans; Williams *et al.* 1993; Nummi & Saari 2003). Rarely, however, has population density been shown to have an effect on adult survival (Dugger *et al.* 1994; Ludwichowski *et al.* 2002; Menu *et al.* 2002; Sedinger *et al.* 2007), which we might expect because adult survival has high elasticity values and should thus be highly buffered against environmental changes induced by population density (see sections above).

Given existing evidence, and following the Eberhardt hypothesis that ungulate ecologists have used to focus their study of density dependence (Eberhardt 1977, 2002; Bonenfant *et al.* 2009), we hypothesise that waterfowl become more robust to the effects of density dependence as they develop into the prime ages of adulthood, but might again become susceptible at older ages; for instance, because of immunosenescence and density-related pathogen transmission (Palacios *et al.* 2011).

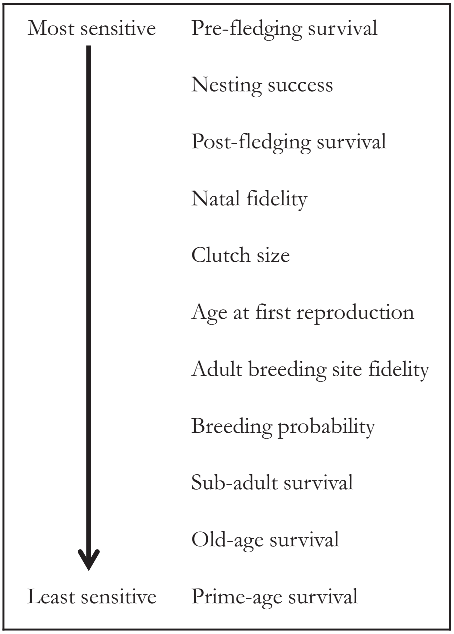

Figure 4. A hypothesised sequence of vital rate sensitivity to density dependence over the age-structured life-cycle of a hypothetical waterfowl species.

For a given waterfowl taxonomic group, the rank-order of vital rate sensitivity to density dependence can be organised as a list (see Fig. 4), but the organisation and presence of density dependence across the life-cycle could shift with life history strategy (*e.g. r–K* selection; MacArthur & Wilson 1967; Pianka 1970) or perhaps more so with "lifestyle" (*e.g.* diet, nest-site preference, mating strategy, *etc.*; Dobson 2007; Sibly & Brown 2007) and prevailing environmental conditions. At this point, these ideas are nascent and are presented here for future waterfowl ecologists to advance or repudiate as science progresses. Knowing where density dependence operates in the life-cycle, and how it varies over time and space will eventually help managers apply actions in the most appropriate seasons, habitats and environmental conditions for achieving desired population responses relative to resource investments (du Toit 2010).

Conclusions

Our understanding of waterfowl population dynamics has come a long way since the middle part of the 20th century. A strong focus on studying vital rates has helped develop and improve population models for several species, and new tools have allowed researchers to identify differences in vital rate contributions to population dynamics across life histories. Progress has been made in research on bottom-up and top-down mechanisms affecting populations, and light has even been shed on the once elusive mechanism of density dependence.

There are nevertheless key gaps that need to be filled in order to sustain healthy waterfowl populations amidst the challenges presented by global change. For example, significant portions of Palearctic waterfowl populations occupy regions where research and monitoring are scarce (*e.g.* Russia and the boreal forest of North America), which makes it difficult to develop scientifically robust studies and management of populations that do not necessarily recognise geographic borders and survey boundaries. We outlined briefly our current understanding of density dependence in waterfowl, and presented a framework for organising an understanding of the key life-cycle stages where density dependence has a significant impact on population dynamics (Fig. 4). Although often assumed in energetic models, explicit studies of density dependence during the staging and wintering periods of the life-cycle are scarce. The cross-seasonal approach to studying life-cycle dynamics may be the best way to fulfil these informational needs (see Sedinger & Alisauskas 2014).

In addition to adaptive management approaches, formal experiments are needed to separate density-dependent from density-independent processes across gradients of resource availability. Long-term observational studies additionally offer the test of time, and are perhaps the best way to understand the complex effects of environmental change and stochasticity on populations (Clutton-Brock & Sheldon 2010). Where possible, experimental and observational approaches should be combined to enhance learning within the adaptive management framework.

The relatively new Integrated Population Model (IPM, not to be confused with "integral" population models) offers an innovative way to combine data from different research approaches to test hypotheses and, importantly, to link information from detailed field studies with large-scale monitoring data to guide adaptive management (Besbeas *et al.* 2002). In addition, by using the constraint that only birth, immigration, death and emigration can affect population abundance, IPMs can combine abundance data with vital rate data in a way that can reduce bias and improve precision in demographic estimates (Abadi *et al.* 2010). Utilising these features, IPMs are already being used to provide a synthetic view of the mechanisms that shape waterfowl population dynamics (Péron *et al.*

2012), and are even being used to study the demographic effects of species interactions at large scales (Péron & Koons 2012). IPMs thus offer a way to model the dynamic mechanisms that affect waterfowl populations and communities at scales that are relevant to managing migratory species. Waterfowl are among the most extensively studied vertebrates on the planet, and we predict that this rich tradition will contribute to great advancements in population ecology, evolution and applied natural resource management in the 21st century.

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