REVIEW AND SYNTHESIS

When density dependence is not instantaneous: theoretical developments and management implications

Irja I. Ratikainen,[1,2]* Jennifer A. Gill,[3] Tómas G. Gunnarsson,[3,4,5] William J. Sutherland[5] and Hanna Kokko[1,2]

[1]Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, PO Box 65 University of Helsinki, 00014 Helsinki, Finland

[2]Centre for Conservation Biology, Department of Biology, Realfagbygget, NTNU, N-7491 Trondheim, Norway

[3]School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

[4]Snæfellsnes Research Centre, University of Iceland, Hafnargata 3, IS-340 Stykkishólmur, Iceland

[5]Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

*Correspondence: E-mail: irja.ratikainen@bio.ntnu.no

Abstract

Most organisms live in changing environments or do not use the same resources at different stages of their lives or in different seasons. As a result, density dependence will affect populations differently at different times. Such sequential density dependence generates markedly different population responses compared to the unrealistic assumption that all events occur simultaneously. Various field studies have also shown that the conditions that individuals experience during one period can influence success and *per capita* vital rates during the following period. These carry-over effects further complicate any general principles and increase the diversity of possible population dynamics. In this review, we describe how studies of sequential density dependence have diverged in directions that are both taxon-specific and have non-overlapping terminology, despite very similar underlying problems. By exploring and highlighting these similarities, we aim to improve communication between fields, clarify common misunderstandings, and provide a framework for improving conservation and management practices, including sustainable harvesting theory.

INTRODUCTION

Population regulation, the process whereby a population shows a tendency to return to its equilibrium, is fundamental to ecology and related fields such as conservation and management. The negative feedback mechanisms that characterize density dependence are essential for such regulation. Density dependence, however, does not necessarily always operate in its most simplistic form, where individuals reside in just one environment. What happens if individuals change environments, possibly repeatedly, during their lives? Such changes can arise in different ways. Environments may be physically distinct, as for migratory species in which the breeding, wintering and migration periods can all have regulatory effects on populations (Webster *et al.* 2002). Species may have life histories that include stages in different habitats, or animals may show temporal variation in resource use, for example, due to strong seasonality. Species with such spatial and temporal variation in individual distribution and resource use are likely to experience density dependence in more than one location or time period. When this is the case, it is important to consider the sequential nature of the regulating events.

Even though sequential density dependence occurs in many different taxonomic groups, such as fish, amphibians, insects and even plants, it is maybe easiest to envisage in migrating birds, which often inhabit very different locations in different seasons. Many migratory bird species have recently declined in abundance, and it has been debated whether conditions during winter, breeding or migration seasons limit population sizes (Sherry & Holmes 1996; Newton 2004, 2006; Mills 2006). However, this discussion

has generally not included the knowledge obtained in more theoretical treatments of sequential density dependence. Ornithologists have, on the other hand, taught us much about another, related phenomenon that occurs in seasonal environments: that individual fitness in one stage may depend on how well the individual did in the stages before (carry-over effects), with potential impacts on population size (Norris 2005; Runge & Marra 2005). Both carry-over effects and sequential density dependence may result in population dynamics that are very different from the simplistic assumption that the lowest carrying capacity should determine population size.

Sequential density dependence has been studied in different contexts, in theory and empirically, but with relatively little overlap between related fields or across taxonomic borders. In addition to having been considered in basic theoretical studies (Fretwell 1972; Kot & Schaffer 1984; Åström *et al.* 1996), it has more recently also been applied to management and harvest theory (Kokko & Lindström 1998; Boyce *et al.* 1999). In this synthesis, our goal was not to provide a complete review of these interrelated topics, but rather to underline the importance of the different processes involved through the seasons or stages, examine the similarities between different systems through theory and empirical examples, and guide further research. We will start by examining the consequences of sequential density dependence in general before we give some specific empirical examples. We will also show how carry-over effects can be incorporated into simple seasonal models, and consider the management implications of these important complications.

THE THEORETICAL BACKGROUND

In this section, we focus on sequential density dependence that results from the simple interaction between population size and the environment, thus we ignore carry-over effects. There are two general ways of modelling sequential density dependence. The alternatives, differential equations with periodic functions (e.g. Holt & Colvin 1997; Kokko & Lindström 1998) and sequentially occurring discrete events of density dependence (e.g. Fretwell 1972; Kot & Schaffer 1984; Jonzén *et al.* 2002a), make use of continuous and discrete-time models, respectively. Differential equation models can often be considered more realistic simply because biologically relevant events, in reality, overlap in time: mortality may occur during the breeding season, for instance. Such models also allow for the possibility that vital rates, such as mortalities or birth rates, vary during a season as densities change, as is the case for salmonids (e.g. Einum *et al.* 2006). Models with discrete events, on the other hand, are intuitively easier to grasp, and they may also be more appropriate, e.g. in cases of two discrete habitats or in migratory species. In addition to these population-level models, sequential density dependence

has also been investigated using individual-based models (e.g. Pettifor *et al.* 2000).

A simple discrete model of sequential density dependence

Our basic example assumes two seasons, following Fretwell (1972). Consider a population that consists of N_a individuals in the autumn, while the population size in spring before breeding is N_s. We assume the breeding contributes bN_s to the population size, where b is the *per capita* reproductive output. Assuming no mortality during the summer, the autumn population size, N_a, must be

$$N_a = N_s + bN_s. \tag{1}$$

Subsequently, we assume that all mortality occurs during winter, so that the following spring population density is

$$N_s = N_a - mN_a. \tag{2}$$

An equilibrium is found when the N_a and N_s of eqns 1 and 2 coincide. To provide a simple example, we let both reproduction and mortality be linearly density-dependent:

$$b = B - \beta N_s \tag{3}$$

and

$$m = M + \alpha N_a. \tag{4}$$

Here, B is the maximum *per capita* birth rate (achieved in a small summer population), M is the minimum *per capita* death rate (achieved in a small wintering population), and α and β determine the strength of density dependence in mortality and reproduction, respectively. The annual dynamics are depicted in Fig. 1. The equilibrium is found by substituting the right-hand side of eqn 2 for N_s in eqn 1:

$$N_{a,t+1} = N_{a,t} - mN_{a,t} + b(N_{a,t} - mN_{a,t}), \tag{5}$$

where t denotes the year. This is achieved if $m + b = bm$. For other and more elaborative examples of correct sequential treatments, see e.g. Fretwell (1972), Kot & Schaffer (1984), Rodriguez (1988) and Åström *et al.* (1996).

PREDICTIONS AND EMPIRICAL RESULTS

Sequential density dependence often features *compensation* (absence of compensation is described as *additive mortality*): in the above example, additional mortality that decreased the spring population size would be compensated by higher than usual breeding output, likewise lower than usual breeding success would find its compensation in higher than usual survival in the subsequent season. In the context of seasonal events this phenomenon has been given the name 'seasonal compensation' (Boyce *et al.* 1999; Norris 2005).

The simple definition of *overcompensation*, which we follow here, is compensation that is so strong that an initial removal of individuals leads to a higher population size
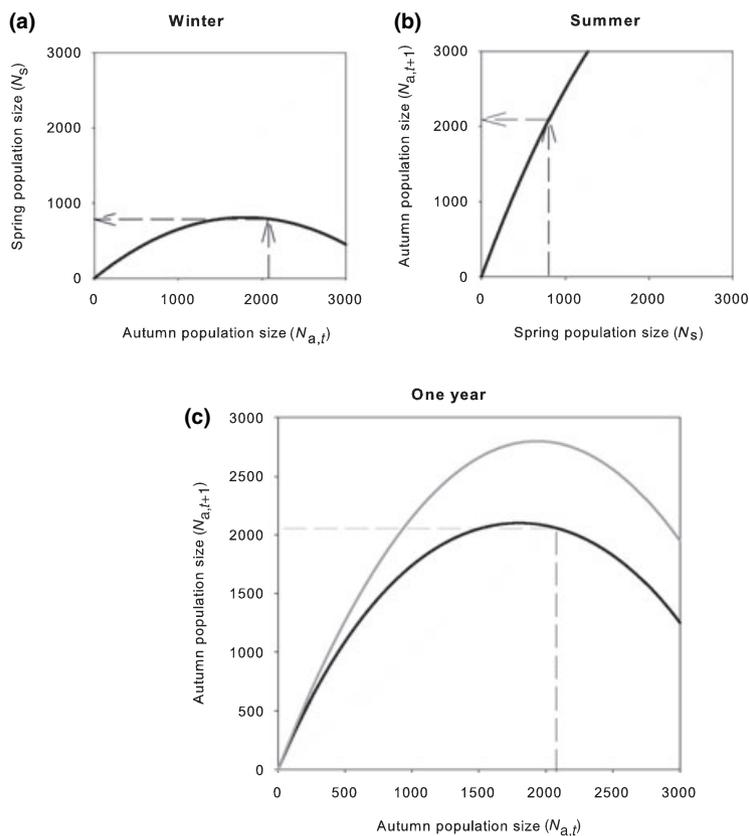
Figure 1 Population size after 1 year is a product of processes in two seasons. (a) First mortality reduces population size from autumn to spring (thick black line) according to $N_s = N_a - mN_a$ and $m = M + \alpha N_a$ (all variables are explained in the main text; $M = 0.1$; $\alpha = 0.00025$). (b) Reproduction then increases population size from spring to autumn (thick black line) according to $N_a = N_s - bN_s$ and $b = B - \beta N_s$ (all variables explained in the main text; $B = 2$; $\beta = 0.0005$). (c) The equilibrium population size is found when population size is the same after 1 year (where the thick black line crosses the dotted line), i.e. when the absolute population increase in summer [found by following the arrows in (a)] is the same as the absolute decrease in winter [found by following the arrows in (b)]. The thick grey line illustrates the equivalent change in population size from one autumn to the next in a non-sequential scenario. The total change in population size is here calculated as $N_t = N_{t-1} + bN_{t-1} - mN_{t-1}$ (b and m defined as in the sequential density dependence scenario and the same values for M, α, B and β were used for the purpose of comparison). In this non-sequential scenario equilibrium is found when $b = m$, i.e. when the *per capita* productivity during the breeding season is the same as the *per capita* mortality in the winter. In this example *per capita* winter mortality stabilizes at 0.616, while *per capita* net summer breeding output was 1.604 at equilibrium in the sequential density dependence scenario.

(measured at some later stage) than would have otherwise been reached. For example, experimental harvesting of soil mite *Sancassania berlesei* eggs led to an increase in the number of adult mites, indicative of overcompensation (while harvesting adults led to the completely different result of decreasing the later number of adults; Cameron & Benton 2004). Another example is found in a model (parameterized with both field and laboratory data) of a system where Bewick's swans *Cygnus columbianus bewickii* graze on fennel pondweed *Potamogeton pectinatus* tubers. This mortality is seasonal because of the migratory habits of swans and, while it decreases the density of *Potamogeton* ramets sprouting next spring, the predicted density of tubers produced in the following autumn is increased (Jonzén *et al.* 2002b).

Models of sequential density dependence show some surprises regarding the strength of compensation. Over-compensation is a common outcome particularly in discrete-time models, which means that the equilibrium population size can increase with additional mortality (Boyce *et al.* 1999). However, whether such strong responses actually occur in natural populations has been the subject of a long and intensive debate, in particular for game species for which questions as to whether mortality is additive, compensatory or overcompensatory have obvious manage-ment implications (see section Harvesting and management implications below).

For plant populations constrained by resources, compen-sation can be absolute so that any loss in density at one time

will be completely compensated by growth in later stages. This is the famous 'self-thinning principle' (White 1981), a rule that plant populations that use limiting resources cannot increase the mean weight of individuals without reducing the mean density. This 'thinning line', which is the relationship between mean weight and mean density, then constitutes an equivalent of a carrying capacity. A similar approach has been adopted for the barnacle *Semibalanus balanoides* and mussel *Mytilus edulis* where the same principles of packing for space apply (Hughes & Griffiths 1988). Application of this principle to the grasshopper *Chorthippus brunneus* (Begon *et al.* 1986) and salmonid fishes is more controversial (Armstrong 1997; Armstrong & Nislow 2006) especially as the original constraint of physical packing no longer applies. In salmonid populations there is a strong pattern of reduced densities in later stages, and the additive vs. compensatory debate from the harvesting literature has been replaced by a contrast between self-thinning and the 'early critical period' (ECP) argument. The ECP argument states that the high mortality during the transition from early life stages to independent foraging (the ECP) is not followed by any density-dependent survival, and thus the ECP constitutes a population bottleneck (Armstrong & Nislow 2006). The self-thinning principle, on the other hand, would include compensatory mortality in later stages.

The timing of population limitation often implies different responses to stochastic events. A model of two seasons with nonlinear density dependence shows that summer (rather than winter) limitation can reduce population vulnerability to stochastic events (Payne & Wilson 1999). This applies particularly to long-lived species with low breeding rates, because they take longer to recover from short-term mortality events compared to events of reproductive failure (Payne & Wilson 1999). Studies of small rodent populations suggest that they are mostly winter limited; however, the difference between the strength of density dependence in summer and winter seems to be greater in more northerly populations (Stenseth 1999).

Models also suggest that it is winter regulation that leads to the multiannual cycles observed in some of these species, through strong seasonal (and delayed) density dependence (Hansen *et al.* 1999), although the drivers of cycles as a whole are still debated and are probably varied (Stenseth 1999; Turchin & Hanski 2001). A comparison of a fluctuating Soay sheep *Ovis aries* population and a stable population of red deer *Cervus elaphus* also suggests that population cycles can be caused by sequential density dependence (Clutton-Brock *et al.* 1997). The difference between Soay sheep and red deer population dynamics is most likely caused by differences in density dependency of reproduction. Red deer reproduction is sensitive to small increases in population size, whereas Soay sheep reproduction is insensitive to all but extreme densities.

This results in very high population sizes in winter which again leads to overcompensatory mortality (Clutton-Brock *et al.* 1997).

Another good example of sequential density dependence is found in black-tailed godwits *Limosa limosa islandica*. The Icelandic godwit population is currently increasing in number and range. This expansion has resulted in a density-dependent process known as a buffer effect, in which an increasing proportion of the population occupies poorer quality habitats. This expansion into poorer quality sites has occurred in both the non-breeding season (Gill *et al.* 2001) and the breeding season (Gunnarsson *et al.* 2005a), thus the sequential density-dependent mechanism currently influencing the godwit population can be described as a double buffer effect, operating in both summer and winter.

A particularly enlightening modelling exercise by Mouquet *et al.* (2005) includes spatial distribution of the large blue butterfly *Maculinea arion*. This species has a complex life cycle that includes strong contest competition between caterpillars on plants and later severe scramble competition within ants nests where the caterpillars eat ant larvae. While strong density dependence can be destabilizing in the case of scramble competition alone, a threshold strength is required for a stable equilibrium population in this model. High rates of fecundity are also destabilizing in this system, because of the overcompensatory response in mortality within ant nests. Simple dynamics generally emerged only when the scramble competition within ant nests was less severe than the contest competition when on plants.

For many species it is usual to consider two or three seasons, and population sizes are measured whenever one season turns into another. However, this assumes that population size variation within a season is unimportant, but such simplification does not always provide sufficient detail. In other words, sequential density dependence is also possible within one season (Åström *et al.* 1996). For example, a season that consists of two temporally distinct stages, each with compensatory mortality, can lead to overcompensation as a whole. Alternatively, the season as a whole may not feature any density-dependent effects on *per capita* rates, because different density-dependent events within the season may have cancelled each other out. For example, Elmberg *et al.* (2005) give evidence for within-season sequential density dependence in mallards *Anas platyrhynchos*. Their introductions of extra mallards to experimental lakes had a significant negative effect on the number of broods hatched, but no effect on the number of older ducklings. Assuming that this is not just a sample size issue, such a pattern can only arise if there is compensation operating between hatching and a time when the ducklings are older. If survival from hatching to the old-duckling stage is not density-dependent, then the negative effect of the *initial* density on the numbers of hatching broods should be

retained and repeat itself in the numbers of ducklings too. As this was not found, there must have been two density-dependent events following each other sequentially, which can, overall, result in complete compensation, i.e. no relationship between initial density and duckling numbers.

Similarly, a laboratory experiment conducted by Vandenbos *et al.* (2006) on fat-head minnows *Pimephales promelas* showed that *per capita* production and survival of eggs were negatively related to initial density of adults, but compensatory growth and survival of the high-density young yielded similar abundance and mean size of all young at the end of the season, irrespective of stocking density (a result reminiscent of 'self-thinning' in plants). There are important practical applications of these studies, for example, stocking of fish at higher densities may yield very little extra economic benefit if fish 'self-thin' in this way. However, this study also found that lower initial densities did eventually result in larger variation in size, which may affect survival or productivity at later stages. This suggests that carry-over effects, which we have ignored so far in this review, should be included to predict recruitment patterns. We will return to this after we have considered another important issue: the order and duration of events.

Order and duration of events

Perhaps the most important lesson from sequential density dependence modelling is that the order of the different events matters (Fig. 3). This can be illustrated by adding a third event, e.g. harvesting, to the simple model outlined above. Following Jonzén & Lundberg (1999) we add hunting mortality, h, such that the *per capita* mortality is density-independent but can happen either before or after winter mortality (a biologically relevant example is autumn vs. spring hunting of waterfowl, Kokko *et al.* 1998). Thus, the removed population is a fraction of either N_s or N_a. For the ease of presentation we now define N_h as the population size after hunting. In the first case (autumn hunting), when hunting occurs before winter mortality but after reproduction, N_h precedes N_a, and N_a is given by eqn 1,

$$N_h = N_a - hN_a, \tag{6a}$$

and

$$N_s = N_h - mN_h. \tag{6b}$$

If hunting occurs after winter mortality but before reproduction (spring hunting), N_s is given by eqn 2, and

$$N_a = N_h + bN_h, \tag{7a}$$

and

$$N_h = N_s - hN_s. \tag{7b}$$

As before, we assume that the *per capita* rates b and m are density-dependent: b in eqn 6a is defined as in eqn 3 while $m = M + \alpha N_h$ in eqn 6b; correspondingly, in eqn 7a we redefine $b = B - \beta N_h$ while m in eqn 7b is defined as previously in eqn 4. The difference is best presented graphically (Fig. 3). Autumn hunting is typically argued as preferable, as it removes individuals who might have died anyway, and compensatory mortality adds to this argument as the removal improves survival of the remaining individuals (Boyce *et al.* 1999). The damaging impact of spring hunting, however, is reduced if there is compensation in the summer, i.e. *per capita* breeding success increases in a smaller population.

Other, more refined models of populations that undergo three mortality/reproductive events in sequence give an indication of the importance of order effects. The size and dynamics of populations is affected by the order of density-dependent events, whether they affect all stages (Åström *et al.* 1996), two (Jonzén & Lundberg 1999; Hellriegel 2000) or just one (Kokko & Lindström 1998; Hellriegel 2000). Early theoretical work attempted to produce general rules, e.g. suggesting that the strength of seasonality can be related to its stabilizing or destabilizing effect on population dynamics (Kot & Schaffer 1984). However, since then theoreticians have examined a wider range of models, and the most accurate summary of the results is that there is an immense repertoire of potential outcomes of sequential models (Åström *et al.* 1996). There may be several equilibria depending on initial population density (Fretwell 1972; Rodriguez 1988; Åström *et al.* 1996), and dynamics may be stable, cyclic or chaotic (Kot & Schaffer 1984; Åström *et al.* 1996; Dugaw *et al.* 2004). It appears that there is no shortcut: researchers will have to examine each system carefully to derive appropriate predictions.

The duration of the mortality periods also determines how the population responds (Kokko & Lindström 1998). This is because different density-dependent processes are in reality likely to overlap in time, and the amount of overlap can affect the density that determines the later population response. If a burst of mortality happens as a discrete event in a period of density-dependent mortality (e.g. a very short and intense harvesting season, or a few days of extreme weather), the effect will depend largely on the timing of the event (early vs. late). The earlier the event, the longer the time for which resources are freed for the survivors to use, and the stronger the resulting compensation. Similar arguments apply for mortalities that occur throughout a prolonged season; individuals that are removed late in the winter (i.e. shortly prior to a new breeding season) are more 'additive' than those removed early. Kokko & Lindström (1998) show how two standard models of density dependence over an annual scale, the Beverton-Holt and Ricker models, can be derived assuming continuous-time resource use over a prolonged mortality period, followed by a birth pulse. Ricker dynamics follows if mortality rates of all individuals are determined by the state of the environment

at the beginning of the overwintering season, while Beverton-Holt can be derived if mortality decreases as competitors die (see also Geritz & Kisdi 2004). Longer harvesting seasons are thus more detrimental, in the sense that the same number of hunted individuals decreases equilibrium population sizes more if the season is long, and the timing of harvesting matters more in latter case in which mortality responds continuously to the number of competitors (Kokko & Lindström 1998).

CARRY-OVER EFFECTS

Carry-over effects are non-fatal effects on individuals during one period that influence success and *per capita* vital rates during the following period (Webster *et al.* 2002; Runge & Marra 2005). For example, brent geese with higher fat-loads on the spring staging grounds produce more offspring after migrating to the breeding grounds (Ebbinge & Spaans 1995). The concept also incorporates any delayed effect of individual 'state' such as parasite load, whether it carries a disease, or the type of habitat the individual is constrained to use (e.g. birds in poor condition that depart their wintering grounds late may not be able to secure a high quality breeding territory). One specific example of a carry-over effect can be severe conditions during migration that will lower individual condition and subsequently affect reproductive output in the following breeding season. This effect is independent of density during the migration and is therefore labelled density-independent carry-over effect.

Density-independent carry-over effects can affect population sizes (e.g. Norris 2005), but they cannot contribute to population regulation. We will therefore focus on density-dependent carry-over effects. Such carry-over effects represent changes in the states of individuals that are determined by the population density in the season when the individuals experienced changes in access to resources, but are expressed in a later season. An example of a density-dependent carry-over effect could be high number of individuals in winter leading to more competition and hence a greater proportion of lower quality individuals in the subsequent reproductive season, which may lead to reduced reproductive output. Reduced productivity will, however, lead to reduced competition in the following winter and thus higher reproductive output in the subsequent breeding season.

A simple model of carry-over effects in a seasonal environment

Density-dependent carry-over effects can be incorporated into sequential density dependence models by allowing functions that relate population sizes before and after a season to depend not only on the density in beginning of the relevant season, but also on that in the preceding season;

in other words the population model now features delayed density dependence. We will provide an illustrative model by expanding our two-season model of sequential density dependence. Remember that population size in the autumn, N_a, is $N_s + bN_s$ after the increase from reproduction (eqn 1), while the spring population size N_s is $N_a - mN_a$ after the reduction caused by winter mortality (eqn 2). For simplicity, we assume no carry-over effects from summer to winter and that m is given by eqn 4, as before. We assume density-dependent carry-over effects from winter to summer though, and now b is still given by eqn 3, but B is now dependent on N_a:

$$B = b_0 - b_1 N_a \tag{8}$$

Now all individuals reproduce poorly in the summer if the population size in the previous autumn was high. The equilibrium conditions can be found by equating the autumn population sizes in the two following years (Fig. 4).

Population consequences of carry-over effects

A central feature of our review is that sequential events can substantially increase the diversity of density-dependent effects, and this diversity precludes the formulation of simplistic general conclusions. Carry-over effects are no exception; they can act either in conjunction with or in the opposite direction of regulatory mechanisms (Norris 2005; Norris & Taylor 2006). This is easiest to explain with an example of seasonal environments. If higher densities during winter imply that more individuals have to overwinter in poor quality sites, then this may not only increase winter mortality (within-season density dependence), but it could potentially also reduce the reproductive output of the surviving individuals, and therefore the total *per capita* reproductive output in the breeding season (density-dependent carry-over effect). In this example density dependence and carry-over effects operate in the same direction, both having a negative effect on population size. However, if more individuals entering the winter season means that the survivors are of higher quality (e.g. if high densities in the beginning of the winter means that most individuals die early in the winter, and the survivors get better access to resources), this could increase *per capita* reproductive rates in the following summer, and immediate density dependence and density-dependent carry-over effects are now working in opposite directions.

Not many models have attempted to incorporate carry-over effects into a sequential density dependence framework, and one of the exceptions (Norris & Taylor 2006) is based on the problematic shortcut of constant overall population size (see Box 1). This problem is avoided in a study using matrix modelling that clearly shows the potential of carry-over effects to decrease populations sizes (Runge &

Box 1: When density dependence is considered instantaneous

A widespread simplifying assumption that is present in older (Williamson 1972; Sutherland 1996, 1998) as well as more recent work (Norris & Taylor 2006) is that the equilibrium population size is that at which the *per capita* mortality rate equals the *per capita* net breeding output rate. However, a *per capita* argument can be mathematically valid only if mortality and breeding output depend on the same population size. Yet population sizes cannot remain constant throughout the year if mortality and breeding are at least partially seasonally non-overlapping. To avoid inconsistencies, the assumption of equal rates should therefore not be made in models of two or more seasons.

A simple numerical example shows the effect of the assumption of equal vital rates on population equilibrium. Consider a population that comprises 1000 individuals in the autumn, and 20% of individuals die in the winter (mortality = 0.2). The spring population size is therefore 800 individuals. If *per capita* reproduction in the summer is the same as *per capita* winter mortality (0.2), the autumn population size is 960, i.e. less than the original 1000. Despite the equal rates of birth and death, the population is not at equilibrium. If, however, mortality and reproduction happened simultaneously, then they could both be based on the same population size, and equal vital rates would indicate population equilibrium. The effect can more generally be shown in the simple discrete model of sequential density dependence (eqns 1–5). In this model, *per capita* breeding output (b) only equals *per capita* mortality (m) when $b = m = 0$, which is biologically impossible in an extant population. This argument also applies regardless of

scale, i.e. if one considers relative rather than absolute population sizes.

There is some work acknowledging that $b = m$ is not generally true at equilibrium (Norris 2005), yet such work and a subsequent review (Newton 2006) and textbooks (Begon *et al.* 1996; Goss-Custard & Sutherland 1997) have thereafter accepted the simplification $b = m$ without assessing the consequences. The difference between equilibrium population sizes in a sequential density dependence framework and an equal-rate framework is illustrated in Fig. 2. In this example the equal-rate framework (non-sequential density dependence) generally overestimates the equilibrium population sizes as counted in autumn. With seasonality, the density-dependent impacts in one season will be lower than for equal rates as the population has already been reduced in the other season. This effect is stronger when winter density dependence is strong, or when both summer and winter density dependencies are weak. Note that the stage at which the population is censused can influence conclusions regarding population size. If there is density dependence in all periods, the effects of the last period before the census may appear disproportionately important, as they will have larger impact on the censused population size.

This highlights the problems that can arise if full sequential dynamics with all relevant population sizes are not properly characterized. We therefore conclude that the simplifying assumption of equal rates should not be used whenever models consider explicitly sequential events. In addition to being mathematically inconsistent, the assumption can lead to inflated estimates of population size (Fig. 2) and oversimplified dynamics (see Åström *et al.* 1996), both of which can have severe consequences for management strategies.
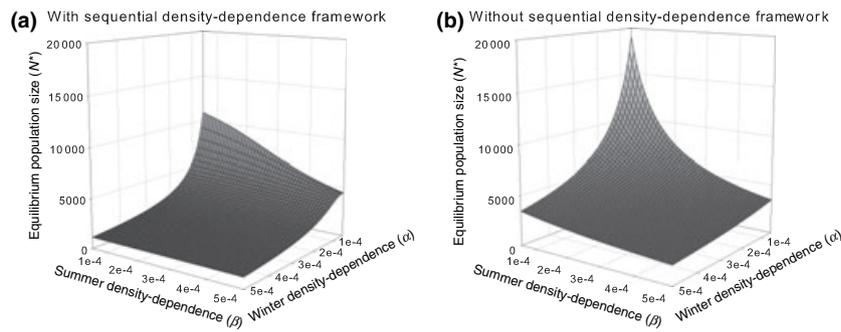
Figure 2 The equilibrium population size for a range of different density dependencies (α and β both range from 0.00005 to 0.0005) in two sequential events in (a) a sequential density dependence framework (given by eqns 1–4 in the main text) and (b) a non-sequential density dependence framework [population size at year t, $N_t = N_{t-1} + N_{t-1}(B - \beta N_{t-1}) - N_{t-1}(M + \alpha N_{t-1})$]. Generally, the non-sequential density dependence framework overestimates the equilibrium population size, and this effect is larger when winter density dependence is strong, or when both winter and summer density dependencies are weak. All equilibrium population sizes are calculated by solving for $N_t = N_{t-1}$ ($N_{a,t} = N_{a,t-1}$ in the sequential density dependence framework). Other parameters are $M = 0.1$ and $B = 2$.

Effect of extra density-independent mortality on equilibrium population size
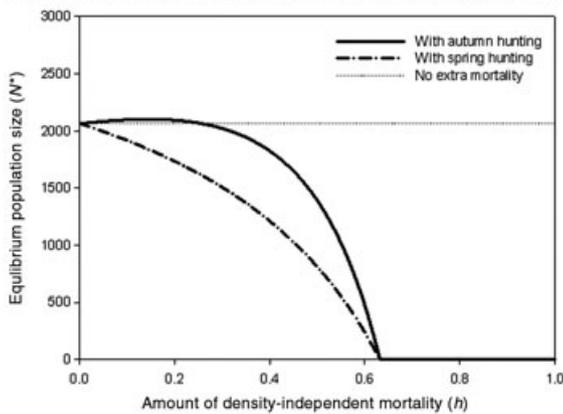
Figure 3 Equilibrium population size in a sequential system is affected by the amount of additional density-independent mortality (e.g. hunting). In this example, the population experiences two seasons; winter mortality (with autumn hunting: eqn 6b in the main text, or spring hunting: eqns 2 and 4 in the main text) and summer reproduction (autumn hunting: eqns 1 and 3, or spring hunting: eqn 7a). In addition, there is also density-independent hunting mortality, h. The population size after given by eqn 6a or 7b for autumn and spring hunting, respectively. The equilibrium population size, N^*, is found by solving for equal autumn population size after all three events. When hunting is added before the winter mortality (solid line) a small amount of additional density-independent mortality can increase the equilibrium population size (overcompensation). In this scenario the maximum equilibrium population size is reached when $h = 0.146$. If hunting is added after the winter mortality but before summer reproduction (dashed line), any hunting will reduce the equilibrium population size. Parameters in this example are set to $M = 0.1$, $B = 2$, $\alpha = 0.00025$ and $\beta = 0.0005$.

Marra 2005). The carry-over effects in this model are, however, very simple (indeed, the simulations replicate the double buffer-effect closely), and changes in parameter values were not explored to any extent. Modelling also shows that the effect of density-independent carry-over effects on population responses to habitat loss depends on the quality of the habitat lost (Norris 2005). In this model, carry-over effects can increase the population decline because of the loss of high quality habitat, but when low quality habitat is lost carry-over effects may actually buffer the population decline (Norris 2005).

Evidence of carry-over effects in nature

A series of studies on American redstarts *Setophaga ruticilla* show good evidence of carry-over effects from winter habitat to summer breeding: birds that over-winter in good habitat migrate earlier, arrive earlier, are in better condition both before and after migration, and fledge more young than birds over-wintering in poor habitat (Studds & Marra

Carry-over effects
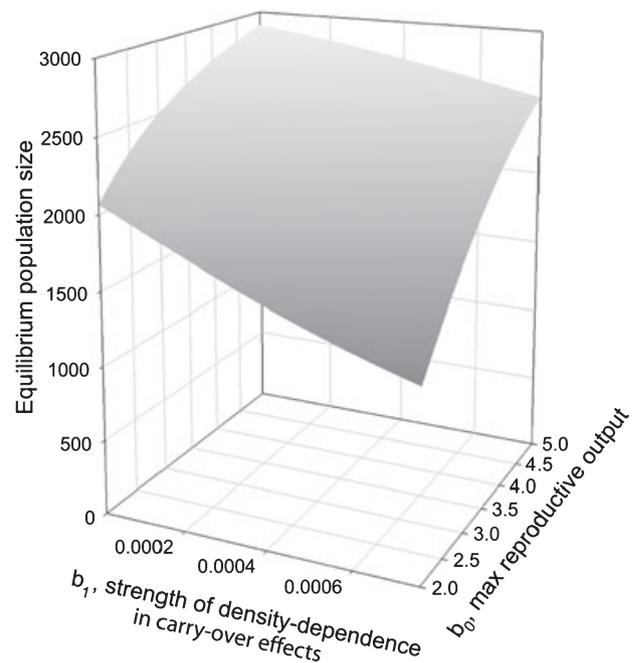
Figure 4 Equilibrium population sizes in a population with carry-over effects. Equilibrium population sizes decline when density dependence increases, but this effects is more pronounced when the maximum reproductive rates are high. Equilibrium population sizes in this example are found by solving eqn 5 in the main text, with B dependent on N_a: $B = b_0 - b_1 N_a$ according to eqn 8 in the main text. Strength of density dependence in the carry-over effect varies between 0 and 0.00075, while the maximum reproductive output varies between 2 and 5. Other parameters in this example are the same as in the other figures: $M = 0.1$, $\alpha = 0.00025$ and $\beta = 0.0005$.

2005 and references therein). There are also indications that male American redstarts carry-over effects from parental investment to location of moulting and feather colours, which can affect access to good habitat and female mate choice in subsequent seasons (Norris *et al.* 2004). Density-independent carry-over effects have also been shown in pied flycatchers *Ficedula hypoleuca,* where overall breeding success was higher after favourable wintering weather conditions (Laaksonen *et al.* 2006).

Carry-over effects can encompass processes ranging from individuals being randomly distributed in a given season and the quality of resources to which each is exposed determining individual fitness in the subsequent season, through to individuals consistently experiencing conditions of similar rank quality in all seasons (termed *seasonal matching* by Gunnarsson *et al.* 2005b). Seasonal matching of the relative quality of sites used by individuals in different seasons may have the most profound effects on population dynamics, for example, by increasing fitness variance across

a population and influencing effective population size (Gunnarsson *et al.* 2005b). A long-term study of Icelandic black-tailed godwits has provided empirical evidence for seasonal matching by tracking marked individuals throughout the year and at the population scale (Gunnarsson *et al.* 2005b). Individual godwits that occupy good quality breeding habitats also tend to occupy good quality winter locations, whereas individuals from poor quality breeding habitat tend to occur in poor quality winter sites. This seasonal matching has clear implications for population and evolutionary processes, as some individuals consistently benefit from breeding in higher quality sites and wintering in areas where survival is higher.

The relatives of carry-over effects: delayed density dependence and maternal effects

Beckerman *et al.* (2002) classified six ways in which an environmental condition could lead to a population response. The condition could be lethal or non-lethal (e.g. a parasite infection that reduces fecundity, but does not result in death), and the life-history response can be immediate or delayed. If the life-history response is immediate, the population response can be either immediate or delayed. If, on the other hand, the life-history response is delayed the population response must logically be delayed as well. If we place carry-over effects in this context, we can see that they are very similar to what Beckerman *et al.* (2002) classified as non-lethal effects of the environment with delayed life-history effects. Carry-over effects will thus give rise to a delayed population response, which is usually density-dependent. Note that carry-over effects are normally defined as an effect from one season to the next but, as in studies of delayed density dependence, the time-scales involved matter less than the general conclusion that delays can diversify the range of population dynamics observed.

Even though there is a dearth of data and modelling devoted to understanding population consequences of carry-over effects, there are lessons to be learned from similar phenomena. There is a huge literature on delayed density dependence and, as we showed above, these are a natural consequence of density-dependent carry-over effects. Delayed density dependence at the population level has been investigated much more thoroughly than carry-over effects at the individual level (but see Beckerman *et al.* 2003; Benton *et al.* 2005). The importance of delayed density dependence stems from its relevance to the debate of causes of population cycles, particularly in rodents (Stenseth 1999), and is also suggested as an explanation for population cycles in other taxa such as insects (Rossiter 1991; Ginzburg & Taneyhill 1994) and plants (Crone & Taylor 1996; Gonzalez-Andujar *et al.* 2006).

The difference between the two concepts is the level at which they are defined. Carry-over effects are defined at the individual level, but have implications for the population level. Delayed density dependence, on the other hand, is defined at the population level as an effect of density in a previous period on population growth. The reason for this difference in the level of definition may very well have its roots in the different study traditions of fields in which these terms have been invoked to explain patterns. In rodent population studies, population dynamics has traditionally been studied by tracking population sizes. Birds, for which carry-over effects have been studied, are more often tracked at an individual level, making it possible to include effects of a previous season which cannot necessarily be detected at a population level.

Models of delayed density dependence show what one might intuitively expect: in contrast to direct density dependence, delayed density dependence can destabilize population dynamics and often leads to cycles (May 1981). More specifically for rodents, delayed density dependence in reproductive season length alone can lead to population cycles (Smith *et al.* 2006). However, it is hard to draw more specific knowledge of carry-over effects from the rodent-cycle literature, since there is a difference of time-scales: rodent cycles are typically analysed based on previous years' densities (Stenseth 1999), but carry-over effects are often documented as a response to density in the previous season within the same annual cycle.

There is promise that different research traditions could be merged, because the causes behind delayed (second-order) dynamics at the population level have already been much debated. In the rodent literature, three hypotheses have been proposed as likely explanations for delayed density dependence (Turchin & Hanski 2001): maternal effects, food and predation. Food and predation are trophic interactions that are common explanations for density dependence in general, and could obviously also work as causes of delayed density dependence provided there are time lags (e.g. predator numbers take a while to increase or decrease after changes in prey number). Of course, some aspects of delays should not be equated with carry-over effects: a change in the abundance of predators, for instance, is perhaps more usefully classified as a change in the environment rather than in a rodent's own state.

Maternal effects as drivers of delayed life-history effects share properties with carry-over effects. Maternal effects are normally defined very broadly as any non-genetic similarities between offspring of the same mother (Futuyma 1998). As with carry-over effects, such maternal effects and the related cohort-effects can be density-dependent or density-independent, and they can affect individual performance at later stages (Lindström 1999). Experimental studies of soil mites provide good examples of these processes. Maternal

investment in offspring often forms a trade-off between number and quality, and this will again drive variation in the competitive environment offspring face upon birth. Beckerman *et al.* (2006) provide evidence that the time to hatching in soil mite eggs is a density-independent maternal effect, while the proportion recruiting is mainly explained by juvenile density, which is an effect of maternal investment. An excellent example of a long lag in the effect of a maternal effect is provided by another experiment on soil mites, where grandmaternal effects on several fitness-related traits could be both stronger and could even operate in the opposite direction of maternal effects (Plaistow *et al.* 2006). Similarly, clutch size manipulations in collared flycatchers *Ficedula albicollis* influenced the recruitment of grandoffspring (Gustafsson & Sutherland 1988).

The clearest difference between carry-over effects and maternal effects is the time-scale at which they are typically applied. Maternal effects are acting from one ontogenetic stage to any number of later stages, while carry-over effects are usually considered to act from one season to the next. However, there is nothing in the definition of carry-over effects that prevents longer lasting influences. The lessons to learn from the enormous literature addressing maternal effects are that they can, just as any other type of delayed density dependence, cause population cycles (Ginzburg & Taneyhill 1994; Benton *et al.* 2001) or even more complex dynamics (Benton *et al.* 2001), much in line with our general conclusions regarding sequential density dependence.

FURTHER COMPLICATIONS: INTERACTIONS BETWEEN STAGES

Animals that go through one or more ontogenetic changes, often with a corresponding change in habitat, are excellent systems in which to study density dependence, and they include insects, amphibians, fish, marine invertebrates and parasites. Density dependence can manifest itself in different ways in different stages, e.g. hatchlings may be affected by negative density-dependent survival, while older individuals living in dense populations may have reduced weight gain or increased dispersal rate (Einum *et al.* 2006).

An important additional complication for those species that have different stages coexisting is that effects of different densities at different stages may interact. An elegant experiment with soil mites showed that a reduction in density of one developmental stage can have a range of effects from negative to no effect and positive effects on density in other stages (Cameron & Benton 2004). Possible reasons for this include effects similar to those found in trophic interactions: if stage 1 competes with stage 2 and stage 2 with stage 3, then a large number of stage 3

individuals may reduce those found in the intermediate stage 2, which in turn makes life easier for stage 1 individuals. Numerous other examples of density-dependent interactions between different life-history stages exist, especially from fish (e.g. Einum *et al.* 2006; Vandenbos *et al.* 2006), but also from other taxa.

Cannibalism is often mentioned as a reason for such density-dependent interactions between cohorts (e.g. Claessen *et al.* 2004). In the snow crab *Chionoecetes opilio*, density-dependent cannibalism between cohorts regulates growth and mortalities in junior cohorts (Sainte-Marie & Lafrance 2002). In the *Tribolium* beetles between-stage cannibalism is also an important regulating factor (Caswell 2001 and references therein). Strong density-dependent intercohort effects are also found in the salamander *Salamandra salamandra* (Eitam *et al.* 2005). In that case the mechanism is not clear but competition and cannibalism are suggested as possibilities. Most such studies focus on the effect of one cohort on another in isolation, and further studies on the population consequences of such effects in combination with intracohort sequential density dependence would be both interesting and challenging.

HARVESTING AND MANAGEMENT IMPLICATIONS

An example of how a simple discrete model of sequential density dependence can be used in practice is provided by Ebbinge *et al.* (2002). They found that brent geese *Branta bernicla* reproduction was density-dependent but adult survival was not. By analysing their seasonal model with the estimated vital rates they predicted that the equilibrium maximum population size was already reached. The result is particularly valuable for planning sufficient protection of habitat and for farmers that do not have to fear a further increase in population size and thus economic loss because of agricultural damage.

Much of harvesting and management theory is concerned with predicting population responses to the removal of individuals, or the removal (or addition) of important resources such as food or habitat. In light of the above theory it is clear that sequential density dependence and carry-over effects have the potential to dramatically change population responses: the effects of removing individuals is usually season-specific, and resources are typically needed at specific periods of the year or by specific life-history stages. The population-level effects of sequential density dependence and carry-over effects are variable, but one recurring theme is that these models often show diverse and complex dynamics (e.g. Kot & Schaffer 1984; Rodriguez 1988; Åström *et al.* 1996). This is especially important for managing small populations, when population fluctuations can make the population more prone to extinction by stochastic events.

Harvesting and pest control

Sustainable harvesting often appears to be trying to balance two completely opposing targets: cause minimal damage to populations while also maximizing yield. Sustainable harvesting is only possible when populations respond in density-dependent ways, i.e. one or another vital rate compensates for the increased mortality caused by human action. Much ink has been spilled over whether hunting mortality is compensatory or additive (Pöysä *et al.* 2004 and references therein). While this is obviously important, it should be kept in mind that the sustainability of both compensatory and additive mortality scenarios are influenced by whether breeding output compensates later for reduced breeding populations. Harvesting theory, in other words, should be strongly affected by the idea of sequential density dependence.

Two important points emerge. Firstly, sequential density dependence predicts that timing aspects, not just the total number of individuals taken, are crucial, because the degree of compensation is dependent on the timing and length of the harvesting period (Kokko & Lindström 1998; Choisy & Rohani 2006). Secondly, sequential density dependence can lead to the counterintuitive scenario of overcompensation, where it can be beneficial to a population (in terms of equilibrium numbers) if it is subjected to a harvesting pressure (e.g. Boyce *et al.* 1999).

Consider the first point, assuming that there is little compensation during the breeding season. Harvesting mortality generally has a tendency to turn from compensatory towards additive as the non-breeding season progresses. These shifts can be rapid, which means that simplistic models with a pulse harvest immediately after breeding can seriously overestimate the sustainability of a given harvest, and lead to biased estimates of compensation itself, when in reality individuals are not all taken that early (Kokko 2001). An example of the sensitivity of populations to late losses is seen in eiders *Somateria mollissima*, in which bycatch in fishing gear can cause substantial population damage even if the actual hunting season was scheduled for a sensible time of the year (Merkel 2004).

The complications of timing aspects are also well illustrated by the question of when to control European rabbits *Oryctolagus cuniculus* or, conversely, how to hunt them sustainably (Angulo & Villafuerte 2004; Calvete *et al.* 2005). Control programmes are most efficient during a season with declining rabbit numbers, i.e. prior to reproduction when mortality behaves most additively (Angulo & Villafuerte 2004 and references therein). The opposite goal of conserving wild rabbit populations, on the other hand, places emphasis on hunting after the breeding season. In Spain, where rabbits reproduce in the winter, the optimal harvest period for sustainability may thus be in post-breeding spring popula-

tions, according to an initial analysis (Angulo & Villafuerte 2004). Calvete *et al.* (2005), however, point out complications of the story: autumn hunting tends to be biased towards individuals with minimal demographic value (juveniles and males). This highlights that when the sex ratio fluctuates over the course of the year – which can easily happen if sexes differ in their mortality and if births are seasonal events – a complete analysis may also require knowledge of sex-specific responses to density (see Rankin & Kokko 2007), not just 'asexual' relations between vital rates and sequential density-dependent events such as our models here.

Timing can also confound other factors in the estimation of consequences of harvesting. This is demonstrated by inclusion of a wildlife disease in a model of harvesting in a seasonal environment. The model shows that harvest can increase disease prevalence and mortality, and therefore cause over-optimistic estimates of the response to hunting (Choisy & Rohani 2006). Again, the timing of the harvest season is crucial for the host population response, because it strongly influences disease transmission. The scentless chamomile *Tripleurospermum perforatum* is an invasive weed in North America and provides another example of the importance of timing. Models parameterized by field data show that only additional late mortality (after flowering) has substantial negative impacts on both number of seeds and biomass at equilibrium (Buckley *et al.* 2001). Moderate levels of additional early mortality or reduced fecundity have low negative impact or can even have positive impact on biomass (Buckley *et al.* 2001). It is therefore crucial that the late stage is targeted for the purpose of weed control.

Turning to overcompensation, our second point of sequential density dependence impacts on harvesting, the counterintuitive outcome (population sizes can be increased by removing individuals) means that it is perhaps under-studied. The topic is clearly important, as overcompensation at work would be wonderful news, e.g. to programmes that aim to protect endangered species by allowing limited trophy hunting. It could also seriously compromise any attempts to control pest species. The experiment on mites by Cameron & Benton (2004), which we described previously, finds sufficient evidence for indirect positive population-level effects of harvesting that the authors conclude that we should pay much more attention to them: after all, they were first shown and discussed by Nicholson (1957) in his classic blowfly study.

The possible destabilizing effects of sequential density dependence can also increase the chance of eradicating unwanted species. There are modelling results concluding that seasonally variable density dependence in vector populations strongly increases extinction risk in malaria parasites *Plasmodium* sp. because it leads to higher fluctuations in parasite prevalence (McKenzie *et al.* 2001). This, of

course, also illustrates the possible danger of seasonality for endangered species.

Habitat loss

Habitat loss is a severe threat to biodiversity. The population dynamics of many endangered organisms is evaluated as if density dependence was not important, which may be an understandable first approximation when current birth and death rates determine whether the immediate population growth rate ensures persistence for the foreseeable future. However, when habitat has been contracted or compromised in terms of quality or spatial arrangement, the remaining individuals may be concentrated into areas such that local densities are high; in other words the density dependence itself tightens as resources diminish (e.g. Achord *et al.* 2003).

For species that inhabit multiple habitats, the population response to habitat restoration by increasing any of the available areas is highly dependent on the structure of the density dependence in the population (Greene & Beechie 2004). When modelling population sizes of Chinook salmon *Onchorhynchus tshawytscha*, Greene & Beechie (2004) tested three different scenarios of density dependence (density-dependent mortality for juveniles or adults and density-dependent migration), and found that population sizes differed markedly and the response to changes in habitat size also varied between the different scenarios. In other words, sequential density dependence is crucial for predicting population response and recommending specific restoration strategies.

The consequence of habitat loss or deterioration will of course depend on the quality of the habitat that is lost (e.g. Norris 2005). In addition, from a seasonal point of view, the consequences are greatest for loss in the season in which density dependence is strongest (Runge & Marra 2005), but in many cases population size is determined by resources in more than one season (e.g. Sutherland & Dolman 1994; Runge & Marra 2005) and thus any habitat loss will affect the population.

It seems that for conservation purposes some of the most successful and accurate models of populations with sequential density dependence are behaviour-based models where the sequential nature of density dependence is implicit (Sutherland & Norris 2002). One example of such a model supports the idea that the effect of habitat loss is dependent on the relative strength of density dependence in different seasons (Pettifor *et al.* 2000). In the case of the geese modelled by Pettifor *et al.* (2000), removal of winter habitat resulted in more severe reductions in population size for brent geese *Branta bernicla* compared to barnacle geese *B. leucopsis*. The same models point out one weakness of this modelling approach: results were highly dependent on

accurate parameter estimation, which can be very difficult in many systems. A better approach for these systems may be population-level models, based on knowledge of spatial and seasonal dynamics.

CONCLUDING REMARKS AND FUTURE DIRECTIONS

In this synthesis, we have highlighted the importance of the sequential nature of density dependence in many, if not most, taxa. Scientists working on different organisms have nevertheless branched off in different directions by focusing on different aspects of very similar problems, and the associated terminology has consequently diverged. We do not argue that the terminology is superfluous, as the phenomena studied are not exactly the same, but rather that communication between fields would be facilitated by improving awareness of the similarities between phenomena with very different names.

Despite these problems, sequential density dependence and carry-over effects have been studied in a range of different empirical systems and theory. A common lesson from most of these studies is that we need to consider sequential events sequentially and take lagged effects into account to understand what is going on in the real world. Short-term experiments may be insufficient for finding population responses to changes in density and, while there are many excellent studies of different aspects of density dependence, we now need to take this one step further and consider how these interact. The outcome of sequential density dependence may also feature further complications that we have not considered here, such as dispersal or migratory connectivity between different subpopulations (Goss-Custard & Durell 1990; Sutherland & Dolman 1994; Holt & Colvin 1997; Hellriegel 2000) and stochasticity (Jonzén *et al.* 2002a).

Future studies in which both within-season and between-season (or stage) density dependence is investigated in the same population are likely to be particularly illuminating to the issues we have highlighted here. More studies on invertebrates, tropical species and other species that live in environments that are not obviously seasonal, would give support to the generality of theory presented. There is also a lack of good theoretical studies that explore the interactions between density dependence within- and between-stages. Finally, there is a clear need to quantify how carry-over effects interact with seasonal density dependence, as this has important implications for the management of populations threatened by habitat loss or changes in resource availability.

REFERENCES

Achord, S., Levin, P.S. & Zabel, R.W. (2003). Density-dependent mortality in Pacific salmon: the ghost of impacts past? *Ecol. Lett.*, 6, 335–342.

Angulo, E. & Villafuerte, R. (2004). Modelling hunting strategies for the conservation of wild rabbit populations. *Biol. Conserv.*, 115, 291–301.

Armstrong, J.D. (1997). Self-thinning in juvenile sea trout and other salmonid fishes revisited. *J. Anim. Ecol.*, 66, 519–526.

Armstrong, J.D. & Nislow, K.H. (2006). Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *J. Zool.*, 269, 403–413.

Åström, M., Lundberg, P. & Lundberg, S. (1996). Population dynamics with sequential density-dependencies. *Oikos*, 75, 174–181.

Beckerman, A., Benton, T.G., Ranta, E., Kaitala, V. & Lundberg, P. (2002). Population dynamic consequences of delayed life-history effects. *Trends Ecol. Evol.*, 17, 263–269.

Beckerman, A.P., Benton, T.G., Lapsley, C.T. & Koesters, N. (2003). Talkin' 'bout my generation: environmental variability and cohort effects. *Am. Nat.*, 162, 754–767.

Beckerman, A., Benton, T.G., Lapsley, C.T. & Koesters, N. (2006). How effective are maternal effects at having effects? *Proc. R. Soc. Lond., Biol. Sci.*, 273, 485–493.

Begon, M., Firbank, L. & Wall, R. (1986). Is there a self-thinning rule for animal populations? *Oikos*, 46, 122–124.

Begon, M., Harper, J.L. & Townsend, C.R. (1996). *Ecology: Individuals, populations, and communities*. 3rd edition. Blackwell Scientific Publications, Oxford.

Benton, T.G., Ranta, E., Kaitala, V. & Beckerman, A.P. (2001). Maternal effects and the stability of population dynamics in noisy environments. *J. Anim. Ecol.*, 70, 590–599.

Benton, T.G., Plaistow, S.J., Beckerman, A.P., Lapsley, C.T. & Littlejohns, S. (2005). Changes in maternal investment in eggs can affect population dynamics. *Proc. R. Soc. Lond., Biol. Sci.*, 272, 1351–1356.

Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999). Seasonal compensation of predation and harvesting. *Oikos*, 87, 419–426.

Buckley, Y.M., Hinz, H.L., Matthies, D. & Rees, M. (2001). Interactions between density-dependent processes population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecol. Lett.*, 4, 551–558.

Calvete, C., Angulo, E. & Estrada, R. (2005). Conservation of European wild rabbit populations when hunting is age and sex selective. *Biol. Conserv.*, 121, 623–634.

Cameron, T.C. & Benton, T.G. (2004). Stage-structured harvesting and its effects: an empirical investigation using soil mites. *J. Anim. Ecol.*, 73, 996–1006.

Caswell, H. (2001). *Matrix Population Models*, 2nd edn. Sinauer Associates Inc., Sunderland.

Choisy, M. & Rohani, P. (2006). Harvesting can increase severity of wildlife disease epidemics. *Proc. R. Soc. Lond., Biol. Sci.*, 273, 2025–2034.

Claessen, D., de Roos, A.M. & Persson, L. (2004). Population dynamic theory of size-dependent cannibalism. *Proc. R. Soc. Lond., Biol. Sci.*, 271, 333–340.

Clutton-Brock, T.H., Illuis, A.W., Wilson, K., Grenfell, B.T., MacColl, A.D.C. & Albon, S.D. (1997). Stability and instability on ungulate populations: an empirical analysis. *Am. Nat.*, 149, 195–219.

Crone, E.E. & Taylor, D.R. (1996). Complex dynamics in experimental populations of an annual plant, *Cardamine Pensylvanica*. *Ecology*, 77, 289–299.

Dugaw, C.J., Hastings, A., Preisser, E.L. & Strong, D.R. (2004). Seasonally limited host supply generates microparasite population cycles. *Bull. Math. Biol.*, 66, 583–594.

Ebbinge, B.S. & Spaans, B. (1995). The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high arctic. *J. Avian Biol.*, 26, 105–113.

Ebbinge, B.S., Heesterbeek, H.J.A.P., Ens, B.J. & Goedhart, P.W. (2002). Density dependent population limitation in dark-bellied brent geese *Branta b. bernicla*. *Avian Sci.*, 2, 63–75.

Einum, S., Keith, L.S.H. & Nislow, K.H. (2006). The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos*, 113, 489–496.

Eitam, A., Blaustein, L. & Mangel, M. (2005). Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools. *Oecologia*, 146, 36–42.

Elmberg, J., Gunnarsson, G., Pöysä, H., Sjöberg, K. & Nummi, P. (2005). Within-season sequential density dependence regulates breeding success in mallards *Anas platyrhynchos*. *Oikos*, 108, 582–590.

Fretwell, S.D. (1972). *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey.

Futuyma, D.J. (1998). *Evolutionary Biology*, 3rd edn. Sinauer Associates, Sunderland, MA.

Geritz, S.A.H. & Kisdi, É. (2004). On the mechanistic underpinning of discrete-time population models with complex dynamics. *J. Theor. Biol.*, 228, 261–269.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001). The buffer effect and large-scale population regulation in migratory birds. *Nature*, 412, 436–438.

Ginzburg, L.R. & Taneyhill, D.E. (1994). Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J. Anim. Ecol.*, 63, 79–92.

Gonzalez-Andujar, J.L., Fernandez-Quintanilla, C. & Navarrete, L. (2006). Population cycles produced by delayed density dependence in an annual plant. *Am. Nat.*, 168, 318–322.

Goss-Custard, J.D. & Durell, S. (1990). Bird behavior and environmental planning: approaches in the study of wader populations. *Ibis*, 132, 273–289.

Goss-Custard, J.D. & Sutherland, W.J. (1997). Individual behaviour, populations and conservation. In: *Behavioural Ecology* (eds Krebs, J.R. & Davies, N.B.). Blackwell Science, Oxford, pp. 373–395.

Greene, C.G. & Beechie, T.J. (2004). Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.*, 61, 590–602.

Gunnarsson, T.G., Gill, J.A., Petersen, A., Appleton, G.F. & Sutherland, W.J. (2005a). A double buffer effect in a migratory shorebird population. *J. Anim. Ecol.*, 74, 965–971.

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M. & Sutherland, W.J. (2005b). Seasonal matching of habitat quality and fitness in a migratory bird. *Proc. R. Soc. Lond., Biol. Sci.*, 272, 2319–2323.

Gustafsson, L. & Sutherland, W.J. (1988). The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature*, 335, 813–185.

Hansen, T.F., Stenseth, N.C. & Henttonen, H. (1999). Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. *Am. Nat.*, 154, 129–139.

Hellriegel, B. (2000). Single- or multistage regulation in complex life cycles: does it make a difference? *Oikos*, 88, 239–249.

Holt, J. & Colvin, J. (1997). A differential equation model of the interaction between the migration of the Senegalese grasshopper, *Oedaleus senegalensis*, its predators, and a seasonal habitat. *Ecol. Modell.*, 101, 185–193.

Hughes, R.N. & Griffiths, C.L. (1988). Self-thinning in barnacles and mussels: the geometry of packing. *Am. Nat.*, 129, 818–829.

Jonzén, N. & Lundberg, P. (1999). Temporally structured density-dependence and population management. *Ann. Zool. Fenn.*, 36, 39–44.

Jonzén, N., Ripa, J. & Lundberg, P. (2002a). A theory of stochastic harvesting in stochastic environments. *Am. Nat.*, 159, 427–437.

Jonzén, N., Nolet, B.A., Santamaria, L. & Svensson, M.G.E. (2002b). Seasonal herbivory and mortality compensation in a swan-pondweed system. *Ecol. Modell.*, 147, 209–219.

Kokko, H. (2001). Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildl. Biol.*, 7, 141–150.

Kokko, H. & Lindström, J. (1998). Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecol. Modell.*, 110, 293–304.

Kokko, H., Pöysä, H., Lindström, J. & Ranta, E. (1998). Assessing the impact of spring hunting on waterfowl populations. *Ann. Zool. Fenn.*, 35, 195–204.

Kot, M. & Schaffer, W.M. (1984). The effects of seasonality on discrete models of population-growth. *Theor. Popul. Biol.*, 26, 340–360.

Laaksonen, T., Ahola, M., Eeva, T., Väisänen, R.A. & Lehikonen, E. (2006). Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos*, 114, 277–290.

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends Ecol. Evol.*, 14, 343–348.

May, R.M. (1981). Models for single populations. In: *Theoretical Ecology: Principles and Applications* (ed. May, R.M.). Blackwell, Oxford, pp. 4–25.

McKenzie, F.E., Killeen, G.F., Beier, J.C. & Bossert, W.H. (2001). Seasonality, parasite diversity, and local extinctions in *Plasmodium falciparum* malaria. *Ecology*, 82, 2673–2681.

Merkel, F.R. (2004). Evidence of population decline in common eiders breeding in Western Greenland. *Arctic*, 57, 27–36.

Mills, A.M. (2006). Winter range compression of migrants in Central America. *J. Avian Biol.*, 37, 41–51.

Mouquet, N., Thomas, J.A., Elmes, G.W., Clarke, R.T. & Hochberg, M.E. (2005). Population dynamics and conservation of a specialized predator: a case study of *Maculinea arion*. *Ecol. Monogr.*, 75, 525–542.

Newton, I. (2004). Population limitation in migrants. *Ibis*, 146, 197–226.

Newton, I. (2006). Can conditions experienced during migration limit the population levels of birds? *J. Ornithol.*, 147, 146–166.

Nicholson, A.J. (1957). The self-adjustment of populations to change. *Cold Spring Harb. Symp.*, 22, 153–173.

Norris, D.R. (2005). Carry-over effects and habitat quality in migratory populations. *Oikos*, 109, 178–186.

Norris, D.R. & Taylor, C.M. (2006). Predicting the consequences of carry-over effects for migratory populations. *Biol. Lett.*, 2, 148–151.

Norris, D.R., Marra, P.P., Montgomerie, R., Kyser, T.K. & Ratcliffe, L.M. (2004). Reproductive effort molting latitude, and feather color in a migratory songbird. *Science*, 306, 2249–2250.

Payne, R.J.H. & Wilson, J.D. (1999). Resource limitation in seasonal environments. *Oikos*, 87, 303–314.

Pettifor, R.A., Caldow, R.W.G., Rowcliffe, J.M., Goss-Custard, J.D., Black, J.M., Hodder, K.H. *et al.* (2000). Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *J. Appl. Ecol.*, 37, 103–135.

Plaistow, S.J., Lapsley, C.T. & Benton, T.G. (2006). Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *Am. Nat.*, 167, 207–215.

Pöysä, H., Elmberg, J., Gunnarsson, G., Nummi, P., Sjöberg, G.G. & Sjöberg, K. (2004). Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? *Oikos*, 103, 612–615.

Rankin, D.J. & Kokko, H. (2007). Do males matter? The role of males in population dynamics. *Oikos*, 116, 335–348.

Rodriguez, D.J. (1988). Models of growth with density regulation in more than one life stage. *Theor. Popul. Biol.*, 34, 93–117.

Rossiter, M.C. (1991). Environmentally-based maternal effects – a hidden force in insect population dynamics. *Oecologia*, 87, 288–294.

Runge, M.C. & Marra, P.P. (2005). Modeling seasonal interactions in the population dynamics of migratory birds. In: *Birds of Two Worlds: the Ecology and Evolution of Temperate-Tropical Migration Systems* (eds Greenberg, R. & Marra, P.P.). Johns Hopkins University Press, Washington, DC, pp. 375–389.

Sainte-Marie, B. & Lafrance, M. (2002). Growth and survival of recently settled snow crab *Chionoecetes opilio* in relation to intra- and intercohort competition and cannibalism: a laboratory study. *Mar. Ecol. Prog. Ser.*, 244, 191–203.

Sherry, T.W. & Holmes, R.T. (1996). Winter habitat quality, population limitation, and conservation of neotropical nearctic migrant birds. *Ecology*, 77, 36–48.

Smith, M.J., White, A., Lambin, X., Sherratt, J.A. & Begon, M. (2006). Delayed density-dependent season length alone can lead to rodent population cycles. *Am. Nat.*, 167, 695–704.

Stenseth, N.C. (1999). Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos*, 87, 427–461.

Studds, C.E. & Marra, P.P. (2005). Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology*, 86, 2380–2385.

Sutherland, W.J. (1996). Predicting the consequences of habitat loss for migratory populations. *Proc. R. Soc. Lond., Biol. Sci.*, 263, 1325–1327.

Sutherland, W.J. (1998). The effect of local change in habitat quality on populations of migratory species. *J. Appl. Ecol.*, 35, 418–421.

Sutherland, W.J. & Dolman, P.M. (1994). Combining behavior and population-dynamics with applications for predicting consequences of habitat loss. *Proc. R. Soc. Lond., Biol. Sci.*, 255, 133–138.

Sutherland, W.J. & Norris, K. (2002). Behavioural models of population growth rates: implications for conservation and prediction. *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.*, 357, 1273–1284.

Turchin, P. & Hanski, I. (2001). Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol. Lett.*, 4, 267–276.

Vandenbos, R.E., Tonn, W.M. & Boss, S.M. (2006). Cascading life-history interactions: alternative density-dependent pathways drive recruitment dynamics in a freshwater fish. *Oecologia*, 148, 573–582.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002). Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.*, 17, 76–83.

White, J. (1981). The allometric interpretation of the self-thinning rule. *J. Theor. Biol.*, 89, 475–500.

Williamson, M. (1972). *The analysis of biological populations*. Edward Arnold, London.