REPORT

Cohort effects and population dynamics

Jan Lindström and Hanna Kokko
Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK
Correspondence: Jan Lindström.
E-mail:
j.lindstrom@bio.gla.ac.uk

Abstract

Cohort effects originate from environmental conditions, and can have long-term consequences for the cohort's performance. It has been proposed that cohort effects tend to increase population fluctuations. However, differences among individuals, which cohort effects introduce into a population, usually have stabilizing effects. There are thus two different predictions regarding the impact of cohort effects on population fluctuations. We argue that it is important to distinguish between environmental variability and its long-term effects on individual quality, and approach the question with a population model that can include or exclude such effects. We show that the influence of cohort effects depends on the inherent dynamics: cohort effects can have stabilizing effects if dynamics are inherently unstable. However, the most common outcome is destabilization whenever cohort effects act on top of inherently stable dynamics. Intriguingly, both alternatives are due to individual differences affecting the structure of density dependence in a similar way.

Keywords

Environmental stochasticity, individual differences, population dynamics.

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INTRODUCTION

A 'cohort effect' is a phenomenon where cohorts of a population differ from each other in some average property, such as fecundity. These differences are often induced by conditions during early development (e.g. Lindström 1999). As revealing cohort effects requires longitudinal data, they are best documented in taxa where these kinds of data are available. For instance, in red deer (*Cervus elaphus*) the average lifetime reproductive success differs among cohorts in both males and females (Rose *et al.* 1999). Marked long-term differences in performance between cohorts have also been found in human studies (Takei *et al.* 1996; Ekbom & Akre 1998), insects (Ohgushi 1991), fish (Wiegmann *et al.* 1997), birds (van der Jeugd & Larsson 1998) and plants (Jones & Sharitz 1998). In natural populations, cohort differences are perhaps most commonly caused by climatic vagaries during early development (Post *et al.* 1997; Lindström 1999), but population density may also have an effect (e.g. Forchhammer *et al.* 2001). Note that there is a conceptual difference between cohort effects and maternal effects (e.g. Ginzburg & Taneyhill 1994; Benton *et al.* 2001) in a population dynamics context. In the case of cohort effects, the individuals subjected to varying external conditions do not necessarily pass on their quality to their offspring, whereas this is the very nature of maternal effects.

Despite the abundance of examples where cohort effects affect reproductive output in a population, it has rarely been asked how these long-term signatures of conditions experienced during early development affect population dynamics. In species with overlapping generations, cohort effects necessarily produce individual differences into the population. Thus, this field has been covered indirectly in studies concerning the role of individual differences in single population dynamics (Łomnicki 1988; Bjørnstad & Hansen 1994; Doebeli & deJong 1999). A predominant conclusion of these studies is that individual differences have a stabilizing effect on population dynamics, or in some cases no significant effect at all without certain additional conditions, such as resource monopolization (Łomnicki & Sędziwy 1989). For instance, a population does not necessarily crash to very low numbers if some high quality individuals can secure enough resources in bad conditions. However, the only studies that specifically addressed cohort effects (Albon & Clutton-Brock 1988; Albon *et al.* 1992) concluded that stochastic variation among cohorts is expected to increase population variability.

The aim of this paper is to address this contradiction and propose a solution to it. We build a model where the quality of the environment varies annually, and this can influence survival, fecundity or both. Likewise, the quality of the birth

year may be 'remembered' in an individual's subsequent survival, fecundity or both, resulting in a cohort effect.

MODEL DESCRIPTION

To be able to distinguish between separate cohorts, we use a discrete time population growth model with overlapping generations. We define a cohort effect as any effect that influences the subsequent survival or reproduction of individuals based on the environmental conditions during the early phase of their life. First, we compare population dynamics with cohort effects with otherwise similar dynamics where environmental stochasticity is absent, leading to deterministic dynamics. Generally, to disentangle any true cohort effect from the effect of 'non-remembered' environmental fluctuations, we must also compare our population model with a null alternative where reproduction and survival depend on the (variable) quality of the environment and on population size in the current year t, but not on the properties of the birth year of each cohort. Therefore, we compare stochastic dynamics with or without cohort effects with each other (and both with deterministic dynamics). In an extreme form of a cohort effect, the current quality of the environment has no direct effect on current reproduction or survival, but only a lagged effect in the presence of cohort effects (i.e. if it influences the properties of individuals that become realized later in life). Similarly, stochastic environmental fluctuations can be allowed to influence dynamics even in the absence of cohort effects. We also include intermediates between these alternatives as this is probably the most likely form of cohort effects in natural populations.

We use the Maynard Smith–Slatkin (1973) form of density dependence for either survival, reproduction or both. We chose this form of representing density dependence for three reasons. First, it gives a wide variety of different kinds of density dependencies and population dynamics. Secondly, of the density dependence functions Bellows (1981) compared, this equation gave an adequate description for a majority of natural data sets examined. Thirdly, it is a non-linear function, which is important as the dynamics of populations consisting of homogenous vs. heterogeneous individuals differ qualitatively only if the expected population growth rate depends non-linearly on individuals' quality (Bjørnstad & Hansen 1994).

We denote population size after reproduction by a vector $N_t = \{N_{i,t}\}$, where i indexes the birth year of individuals, and t the current year. The survival of an individual from year t to $t + 1$ depends on its birth year i,

$$p_{i,t} = \frac{p_0}{1 + \left(a_{i,t} \sum_j N_{j,t}\right)^b} \tag{1}$$

where p_0 is survival in the absence of density dependence (for other parameters see below). The population size after the non-breeding season equals $\sum_i p_{i,t} N_{i,t}$. The fecundity of an individual born in year i is, during the new breeding season $t + 1$,

$$f_{i,t+1} = \frac{f_0}{1 + \left(c_{i,t} \sum_j p_{j,t} N_{j,t}\right)^d} \tag{2}$$

where f_0 is fecundity in the absence of density dependence (for other parameters see below). The new population size in year $t + 1$ is hence obtained as

$$\begin{cases} N_{i,t+1} = p_{i,t} N_{i,t} & \text{for } i < t + 1 \\ N_{t+1,t+1} = \sum_i f_{i,t+1} p_{i,t} N_{i,t} \end{cases} \tag{3}$$

Density dependence acts in a cohort-specific way: $a_{i,t}$ and $c_{i,t}$ specify the strength of density dependence in survival (if $a_i > 0$), fecundity (if $c_i > 0$), or both (if $a_i > 0$ and $c_i > 0$), for each cohort i from year t to $t + 1$. Parameters b and d, altering the shape of density dependence, are assumed constant for simplicity. Note that individuals compete with conspecifics of every age: a cohort effect does not mean that competition occurs only within a cohort.

Next we let either the year quality of the environment, the quality of the individual (determined by environment quality during birth year), or both, affect the performance of individuals. Individuals in poorest condition will suffer most from increasing density. This means that the parameters describing the response to density, $a_{i,t}$ and $c_{i,t}$, will increase with decreasing condition. This may happen either if the current year t is harsh, or if the birth year i was harsh, or both. To compare these effects, we let

$$a_{i,t} = a_0 \exp\{-[\alpha q_i + (1 - \alpha)q_t]\}$$
$$c_{i,t} = c_0 \exp\{-[\alpha q_i + (1 - \alpha)q_t]\}$$

where the year's quality q_t follows a normal distribution, $q_t \sim N(0, \sigma^2)$, with no autocorrelation. The parameters a_0 and c_0 specify the density dependence in survival or fecundity, respectively, when both the birth year and the current year are of average quality. The parameter α ($0 \leq \alpha \leq 1$) scales the importance of the cohort effect as opposed to sensitivity to the current environment. When $\alpha = 1$, an individual's sensitivity to current density is solely determined by conditions it experienced in its birth year. When $\alpha = 0$, current conditions determine density dependence completely and the cohort effect is absent. Naturally, α has no effect for one of the life history traits (survival or fecundity) if the corresponding density dependence parameter (a_0 or c_0) is set to zero.
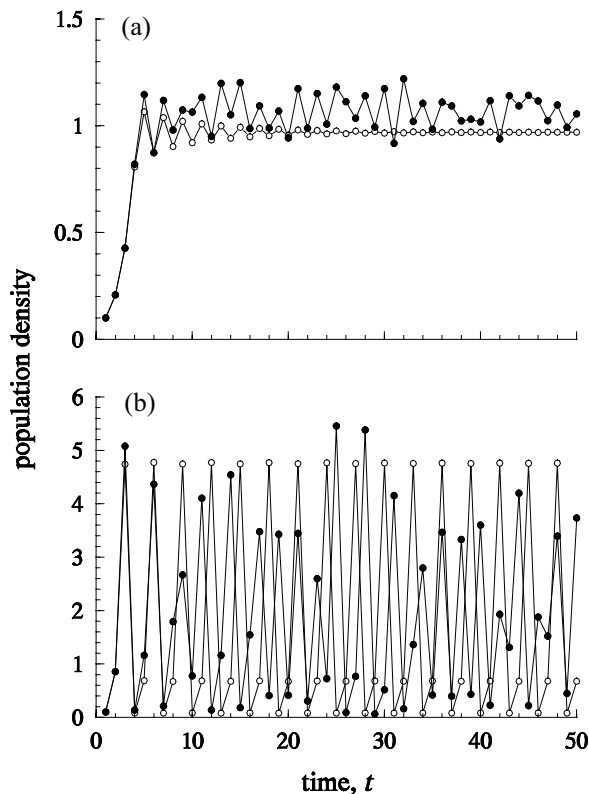
Figure 1 Two examples of population dynamics without (circles) or with (black dots) cohort effects. (*a*) Deterministic dynamics with $p_0 = 0.95$, $b = 4.5$, $f_0 = 1.2$, $d = 2$, a_0, $c_0 = 1$, α, $\sigma = 0$. In the case where cohort effects apply, $\alpha = 1$ and $\sigma = 0.2$. The dynamics that would stabilize at an equilibrium are more variable with the combination of environmental noise and cohort effects. (*b*) Deterministic dynamics with $p_0 = 0.95$, $b = 4$, $f_0 = 8$, $d = 8$, $a_0 = c_0 = 1$, $\alpha = 0$, $\sigma = 0$. Where cohort effects apply, $\sigma = 1$ and $\sigma = 0.2$. The population with deterministic dynamics fluctuates more than the one with noise and cohort effects.

RESULTS

Figure 1 presents two examples of how introducing cohort effects can affect the population dynamics. The population not subject to cohort effects in Fig. 1(a) is intrinsically stable, and the fluctuations here are solely due to transient dynamics. Here, subjecting it to the cohort effect results in markedly stronger variability. By contrast, Fig. 1(b) shows a case where deterministically unstable dynamics (a three-point cycle) results in smaller fluctuations after introducing variation into individual performance according to the quality of the birth year (i.e. the cohort effect). Thus, it is possible that cohort effects can either stabilize or destabilize population dynamics. A further question is whether cohort effects have a weaker or stronger effect on dynamics than similar environmental disturbances, affecting survival and/ or fecundity directly, would have?

A larger set of simulations (Fig. 2) sheds light on this question. Here, we have two comparisons summarized in the same figure. We compare stochastic population dynamics with or without cohort effects with each other, and both with deterministic population dynamics with otherwise identical parameter values. Generally, the variability of stochastic dynamics with or without cohort effects is rather similar, in that adding either form of stochasticity to deterministically unstable dynamics often decreases population variability compared with deterministic dynamics (Fig. 2, negative ΔCV values). However, this general pattern is enhanced if cohort effects are introduced, particularly so when population growth rate and noise variance are high (Fig. 2c, f).

Where do these changes in the effect of intercohort variation arise from? Figure 3 shows the typical shape of the density dependence for $b > 1$. Note, that this is only one example of a very large parameter space, where one can find a qualitatively similar outcome. There are two ways in which cohort effects will influence the shape of the actual density dependence. First, a population of a certain size may consist of cohorts of different qualities, which experience different vital rates from the homogeneous population (depicted by two filled dots surrounding the open symbols representing a homogenous population, Fig. 3). Because of the geometry of density dependence, the *average* vital rate in a heterogeneous population (small dots in central part of Fig. 3) will fall below that of the homogeneous population at low densities, while the corresponding vital rate exceeds it at high densities. This means that the shape of density dependence becomes shallower (low part of Fig. 3) when cohort effects are introduced. Secondly, low population sizes are likely to result from past poor conditions, whereas high population sizes tend to follow good years. If existing individuals tend to remember past conditions in their qualities, low population sizes will tend to consist of poor individuals and high sizes of good-quality individuals. This further reduces population growth rates at the low end of population sizes and vice versa, thus enhancing the pattern in Fig. 3. Figure 2 also shows that when the maximum survival probability, p_0, is high (Figs 2d, e, f), adding stochasticity on the deterministic dynamics dampens the variability more strongly than when p_0 is low (Figs 2a, b, c). This is because the resulting population growth rate is higher when survival is increased, and the deterministic dynamics become more unstable. In this case, adding cohort variation reduces the population variability compared with deterministic dynamics. The difference to the effects of non-lagged environmental stochasticity is at its highest when the environmental variability is high (Fig. 2f).

How, then, do the dynamics respond to the actual density dependence becoming (on average) shallower? Two differ-
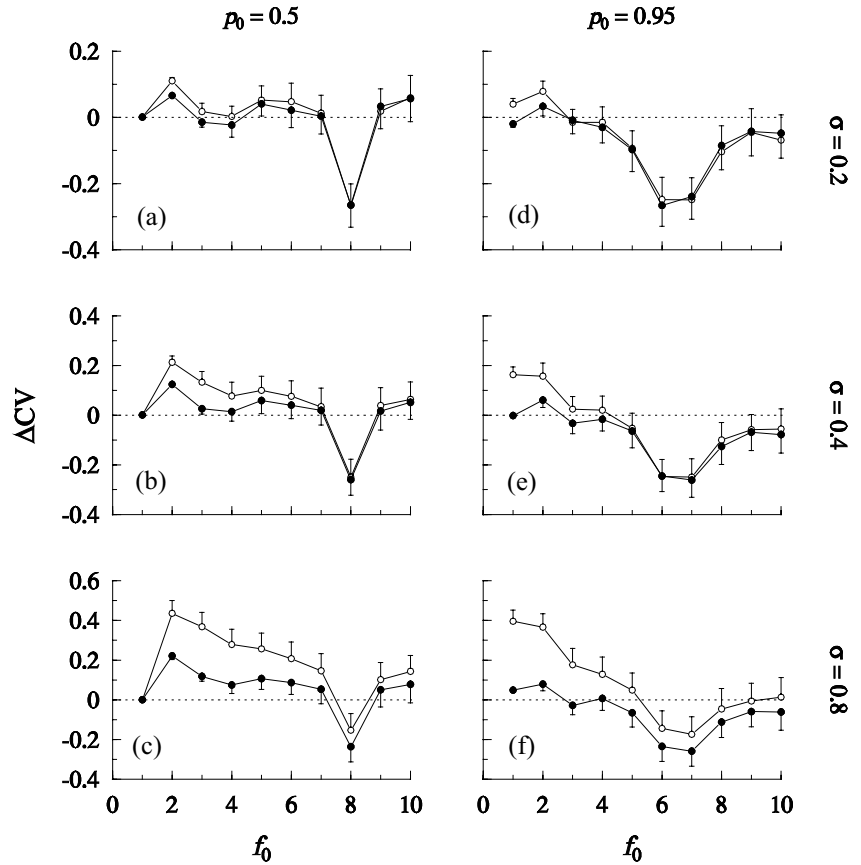
Figure 2 Mean and SE of pairwise difference (ΔCV) between variation (measured as coefficient of variation, CV, over 50 time steps after an initial transition period of 100 time steps) in population sizes of deterministic and stochastic dynamics. Negative values indicate that stochastic dynamics (either with or without cohort effects) decrease variation in population size. Open symbols refer to dynamics without cohort effects ($\alpha = 0$) and filled symbols denote the results for dynamics with cohort effects ($\alpha = 1$). The noise intensity affecting the dynamics with cohort effects increases from top to bottom panels, $\sigma = 0.2$ (a, d), $\sigma = 0.4$ (b, e) and $\sigma = 0.8$ (c, f). In the left hand side panels survival parameter, $p_0 = 0.5$ and in the right hand side panels $p_0 = 0.95$. The x-axis shows the fecundity parameter, f_0. Other parameter values used in these simulations are: a_0, $c_0 = 1$, $d = 2$, and $b = 6$.

ent explanations apply, depending on whether the dynamics are intrinsically stable or unstable. If the original density dependence (Fig. 3) is steep enough to produce deterministic fluctuations, rendering it shallower can result in dynamics becoming relatively more stable. However, if the original slope at the equilibrium is already shallow enough to predict stable dynamics, any fluctuations observed must be due to environmental stochasticity. Then, cohort effects may enhance fluctuations rather than dampen them: lower growth rates at low densities and higher rates at high densities imply a weaker tendency for a population to return towards its equilibrium, once perturbed from it (Fig. 4 confirms this in a simple model without any age structure). This explains the more pronounced transient fluctuations in Fig. 1(b) where cohort effects apply.

Clearly, shallowing the intrinsic density dependence is more important when dynamics are intrinsically unstable, and weakening resilience towards the equilibrium gains importance where fluctuations in relatively stable dynamics are due to environmental variation. However, evaluating their exact balance is difficult, and very likely to be model-dependent. One should also note that our explanation (Fig. 3) is dependent on the particular shape of density dependence studied, although it may be argued that its shape

has generally attractive properties: any vital rate such as survival and reproduction must be bounded between 0 and a maximum value, which easily leads to the inverse S-shape as depicted.

DISCUSSION

We have shown here that cohort effects, introducing individual variation into the population, can have a stabilizing or destabilizing effect on population dynamics. In this sense, cohort effects and maternal effects seem to have similar potential (Benton *et al.* 2001). However, in the case of cohort effects a less long-lasting effect is to be expected as the individual quality is not passed from one generation to the next and hence the time delay between given conditions and the dynamic consequences is shorter. Note, that we use "unstable" interchangeably with "temporally variable", and thus destabilizing effects here refer to increased variance and/or amplitude in population fluctuations. We agree with Bjørnstad & Hansen's (1994) conclusion that the effects of individual variation on population dynamics are highly model dependent. However, at a phenomenological level, we have also shown a rule of thumb for the direction of the
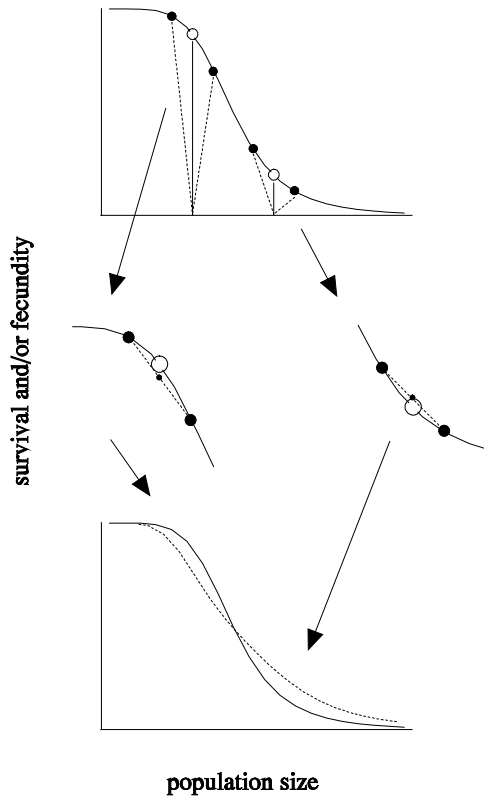
Figure 3 Effects of cohort variation on density dependence. The open symbols give vital rates for a homogeneous population without cohort effects. Black dots depict a situation where 50% of individuals are of higher quality and hence achieve slightly higher vital rates, and 50% are of poorer quality and perform less well. The average vital rate is derived in the middle. This falls below or exceeds the rate of the homogeneous population, depending on the shape of density dependence at different population sizes. The result is lower population growth at low population sizes and higher growth at high sizes, and hence a shallower relationship between density and population growth in the presence of cohort effects (lower part of the figure). The relationship becomes shallower still if low population sizes are predominated by poor individuals (because of past poor years) and vice versa.

Figure 4 A simple simulation shows that 'shallow' density-dependence may enhance stochastic fluctuations in population size. (a), density-dependent maps $N(t + 1) = f(N(t)) \, N(t)$, with either $f(N) = 1.2 \quad (1-(1 + \exp(-0.02(N-300)))^{-1})$ (solid line), or $f(N) = 1.2 \quad (1-(1 + \exp(-0.005(N-550)))^{-1})$ (dotted line). (b) Corresponding dynamics, when population growth is additionally subject to random fluctuations: in each year, $f(N)$ is reduced by 30% with probability 0.25, increased by 20% with probability 0.25, and remains unchanged with probability 0.5. Both types of density dependence experience the same sequence of stochastic changes. The 'shallow' variant (dotted line) recovers more slowly from fluctuations and experiences therefore larger fluctuations (CV = 0.23 vs. 0.39 in solid vs. dotted line). One hundred replicates of such simulations all show the same pattern (sign test, $P < 0.001$).

effect, and the potential mechanisms responsible for the variation. As our results are intuitively explained by the general arguments shown in Fig. 4, they are unlikely to result from the specific model we chose to illustrate the point.

Cohort effects and individual variation tend to increase variation in population fluctuations when the underlying deterministic dynamics is stable. In this case, environmental fluctuations are the ultimate cause of population fluctuations too. Here, fluctuations that produce cohort effects introduce variation to populations in a similar way as environmental fluctuations that affect individuals irrespective of their birth
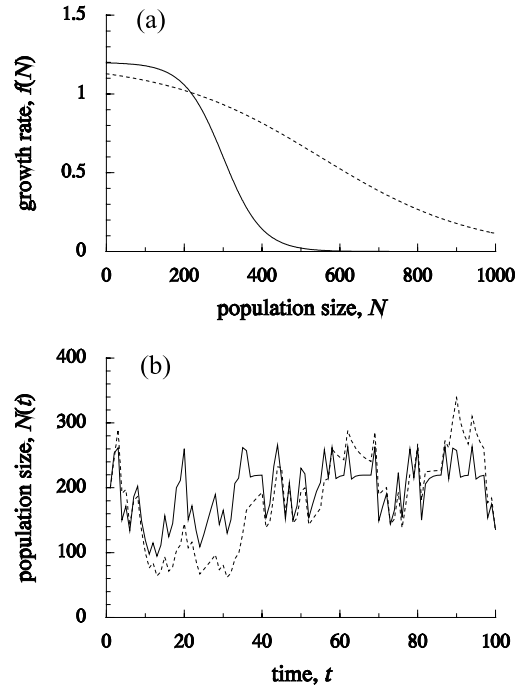
years. An opposite effect is found when population dynamics are inherently unstable. Here, environmental variation has the potential to decrease the temporal variability of a population, and this decrease can become enhanced when cohort effects maintain among-individual variability in condition. Intriguingly, both cases can result from a similar change in the (average) relationship between population density and vital rates. Cohort effects tend to change density dependence to a shallower slope. This leads to opposite effects regarding population variability, dependent on whether variation is mainly caused by environmental stochasticity or intrinsic instability.

This division is useful in that it gives us a starting point in addressing two further questions: Are cohort effects more

likely to stabilize or destabilize population fluctuations in nature? Where should we expect to find these dynamic consequences? Starting with the first question, we conclude that in most natural settings cohort effects and individual variation are more likely to destabilize than to stabilize population fluctuations. Although strongly non-linear density dependencies can be found even in large mammals (Fowler 1981; Lindström et al. 1999), population growth rates in vertebrates are often smaller than those of invertebrates, which reduces relative population variability in vertebrates and tends to produce inherently stable dynamics. Invertebrates, on the other hand, commonly have short life spans and only partially overlapping or non-overlapping generations. They thus lack the opportunity for simultaneous existence of individuals varying in quality, which our modelling suggests to be essential to finding any stabilizing effect.

This also partly answers the second question of where to look for dynamic consequences of cohort effects. Destabilizing effects are probably very common across many taxa. To find stabilizing effects of cohort effects and individual differences, systems with non-linear density dependencies, relatively high potential growth rates and overlapping generations provide the conditions. A natural system, which might serve as an example here, is that of the Soay sheep (*Ovis aries*) in the archipelago of St Kilda (Clutton-Brock et al. 1991; Grenfell et al. 1998; Coulson et al. 2001). Ideally, to assess the importance of cohort effects in shaping the sheep dynamics, this population should be compared with a similar one without long-term cohort effects. While such a comparison is not available, we may still regard the sheep as a candidate which fulfils all prerequisites for finding stabilizing effects of cohort variation. Cohort effects have been shown to exist in this population (Coltman et al. 1999; Forchhammer et al. 2001), density dependencies are non-linear and produce inherently unstable dynamics (Clutton-Brock et al. 1991; Grenfell et al. 1998) and there are sex differences in survival as well as differences between survival of adults and juveniles (Coulson et al. 2001). While the ideal comparison between populations is not available, our long-term prediction is that a sequence of several similar years (in terms of environmental quality) should tend to lead to more pronounced fluctuations than years in which the environment has been variable.

Our finding that cohort variation in vital rates can have stabilizing effects on dynamics, in addition to the perhaps more intuitive alternative of increasing the impact of stochastic fluctuations, arises from the recognition that cohort effects are one way of introducing individual variation into populations. Our model is conservative in the sense that all individuals within a cohort are assumed equal. Whether variability is "aggregated" (i.e. occurs identically in a group of individuals) or "idiosyncratic"

(independent across individuals, in the terminology of Robson et al. 1999) can have major effects on population growth (e.g. Seger & Brockmann 1987; Robson et al. 1999). Further stabilization could be expected if quality differences were allowed to have a random component across individuals. However, such variation does not necessarily have to arise from cohort effects, but could occur independently of environmental quality. According to the definition of cohort effects, some correlation across individuals born to a given cohort is inevitable and we should focus on aggregate properties. This again highlights the importance of separating the effects of variation in quality and temporal stochasticity. Cohort effects surely influence both, but it is the former, arising from whatever reason, which introduces the stabilizing effect.

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