

# What happens if density increases? Conservation implications of population influx into refuges

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## Keywords

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## Abstract

Sudden catastrophic events like fires, hurricanes, tsunamis, landslides and deforestation increase population densities in habitat fragments, as fleeing animals encroach into these refuges. Such sudden overcrowding will trigger transient fluctuations in population size in the refuges, which may expose refuge populations to an increased risk of extinction. Until recently, detailed information about the operation of density dependence in stage-structured populations, and tools for quantifying the effects of transient dynamics, have not been available, so that exploring the extinction risk of such transient fluctuations has been intractable. Here, we use such recently developed tools to show that extinction triggered by overcrowding can threaten populations in refuges. Apart from situations where density dependence acts on survival, our results indicate that short-lived species may be more at risk than longer-lived species. Because dynamics in local populations may be critical for the preservation of metapopulations and rare species, we argue that this aspect warrants further attention from conservation biologists.

## Introduction

Habitat loss is a ubiquitous threat to the world's biodiversity (Wilcox & Murphy, 1985; Soule, 1986). It is largely a consequence of human actions such as deforestation (Brooks *et al.*, 2002), but can also be due to natural causes, for example sudden catastrophes like the south-east Asian Tsunami, or wildfires. Following habitat loss, population densities in unaffected habitats may also change, as fleeing animals encroach into these refuges (Hagan, Van Der Haegen & McKinley, 1996). The magnitude of this 'crowding' effect depends on accessibility of intact fragments to individuals from the destroyed habitats (Grez *et al.*, 2004) and the dispersal capabilities of affected species (Clobert *et al.*, 2001). Despite empirical and theoretical evidence of crowding due to individuals displaced by habitat loss (Fahrig & Paloheimo, 1988; Bierregaard & Lovejoy, 1989; Collinge & Forman, 1998; Debinski & Holt, 2000; Hannon & Schmiegelow, 2002), and increasing recognition of the importance of density dependence (Bonenfant *et al.*, unpubl.data), the implications of transient influxes on population dynamics have rarely been explored from a conservation perspective (but see Ranta, Lundberg & Kaitala, 2006, Chapter 8).

Can an influx of individuals be sufficient to put populations at risk? Demographic rates and transitions are generally agreed to be the outcome of endogenous as well as exogenous processes (Turchin, 1999; McLaughlin *et al.*,

2003). The higher density attained may therefore drive a decrease in demographic rates and transitions. Transient oscillations in population size and a decrease in vital rates due to density-dependent effects such as food shortages might reinforce each other, driving the population towards dangerously small sizes, or towards a population age structure that adversely affects population growth. The risk of this occurring will be determined by a population's dynamics and structure, and specifically density-dependent processes and their potentially complex interactions with the environment. Although estimating density dependence is fraught with difficulty, failure to consider it may lead to overly optimistic predictions of population health (Sabo, Holmes & Kareiva, 2004). The effect of density on dynamics may be mediated by affecting vital rates such as survival or growth either directly through competition for limiting resources (McCallum Kikkawa & Catterall, 2000), or through disease (Wilcox & Elder, 2003), or predation, or behavioural responses to density (Hagan *et al.*, 1996).

In the simplest models of crowding, established populations will be at risk following an influx of individuals only if the addition of one individual leads to the loss of more than one individual from the population. Density dependence in this case is referred to as 'over-compensating'. Theoretically, this condition is associated with non-linear relationships (Hassell, 1975) that occur when populations exceed a threshold level where resources become limiting (Wilcox & Elder,

2003), for example, during drought-induced starvation (Young, 1994). Such non-linear relationships may implicate territoriality and fighting, or 'behavioural dysfunction', where the presence of excess individuals disrupts breeding pairs (Hagan *et al.*, 1996). Longer-lived species are generally believed to show compensating rather than over-compensating density-dependent dynamics. However, detecting the action of such non-linearities can be complex: most populations are structured, that is composed of individuals of different ages, or life stages that experience different demographic rates, and are subject to environmental stochasticity, for example many populations are limited by the abundance of a key resource whose availability fluctuates with season or climate. These can interact to put populations at risk, directly, or indirectly by creating a situation where perturbations from equilibrium may be amplified before decaying, a characteristic described as reactivity (Caswell & Neubert, 2005), which may greatly increase the risk of extinction. Deterministic oscillations due to non-linear dynamics have empirically been shown to be an unexpectedly important determinant of extinction risk in structured populations (Belovsky *et al.*, 1999).

To explore extinction risks associated with incoming individuals, we first explore the effects of population influx on transient population size of density-regulated populations that span a variety of life histories. Then, we develop models based on empirical studies that have estimated the effects of both population density and environmental variability on vital parameters to explore the consequences of population influx on transient population size and extinction risk in real systems, focusing on two species at different ends of a life-history spectrum: arctic ground squirrels *Spermophilus parryii* (Karels & Boonstra, 2000) and Serengeti wildebeest *Connochaetes taurinus* (Pascual, Kareiva & Hilborn, 1997). We conclude by discussing the implications of the results and other conservation aspects of population influx, implications where several trophic levels are involved, and outline areas for future research.

## Methods

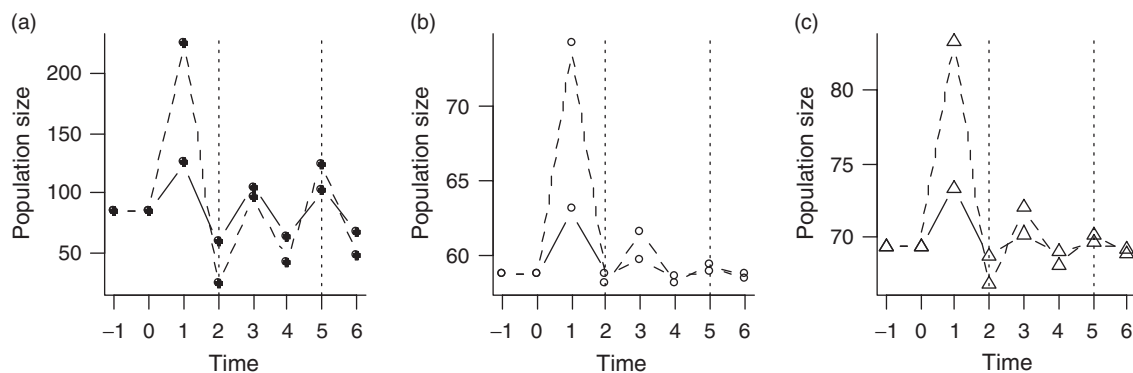
### Transient dynamics in a simplified system

First, to disentangle interactions between density feedbacks and population structure, we created simplified density-dependent age-structured population models assuming birth-pulse reproduction and a post-breeding census, as Caswell & Neubert (2005) indicate that matrix population models based on post-breeding census' can be more reactive to perturbation than those based on pre-breeding census. The matrix structure is

$$A = \begin{pmatrix} 0 & S_a F_1 & S_a F_2 \\ S_j & 0 & 0 \\ 0 & S_a & S_a \end{pmatrix}$$

where  $S_j$  is juvenile survival,  $S_a$  is adult survival, individuals spend one time step as juveniles before they are capable of reproducing, and reproductive output  $F$  can vary with age. A functional form was then chosen such that  $F$ ,  $S_j$  and  $S_a$  could all be altered by the total population density. We defined  $F = F_0 \exp(-p_1 N)$ ;  $S_j = S_{0,j} \exp(-p_2 N)$ ; and  $S_a = S_{0,a} \exp(-p_3 N)$  where  $N$  is total population density and  $F_0$ ,  $S_{0,j}$  and  $S_{0,a}$  are demographic parameters in the absence of density effects. The parameters  $p_1$ ,  $p_2$  and  $p_3$  capture the strength of density effects. The chosen functional form of density dependence allows for over-compensatory dynamics whereby the life history will moderate the strength of such dynamics (e.g. see Fig. 1).

In the classic demographic framework, sensitivity is defined by the absolute change in long-term population growth rate to an absolute change in a parameter value; and elasticity is a proportional change in long-term population growth rate to a proportional change (Caswell, 2001). Recently, techniques for estimating transient sensitivities of population size (and other dependent variables) have become available (Caswell, 2007). With these techniques, and



**Figure 1** Example population dynamics for life histories with (a) low adult and juvenile survival and high fertility ( $S_j = S_a = 0.2$ ,  $F = 25$ , the equilibrium population size is  $N_{eq} = 84$ ); (b) low juvenile survival, high adult survival, and low fertility ( $S_j = 0.6$ ,  $S_a = 0.8$ ,  $F = 3$ ,  $N_{eq} = 57$ ), and (c) high juvenile survival, high adult survival and low fertility ( $S_j = S_a = 0.8$ ,  $F = 3$ ,  $N_{eq} = 69$ ). At  $t = -1$ , populations are at equilibrium, and stage structure is stable. At  $t = 0$ , either 5% (solid lines) or 20% (dashed lines) of the equilibrium population size is introduced into each population. The populations consequently decline. Elasticity plots in Fig. 2 correspond to populations at the dashed vertical lines for  $t = 2$  and  $t = 5$ .

the population model defined above, we calculated the transient elasticity of total population size to parameters describing density dependence following the influx of different numbers of stage 3 adults. We ran this analysis on populations at the equilibrium stage structure, where equilibrium was identified by iterating a population through the matrix model defined above for 100 time steps. At this point, population structure and total size had stabilized. We then introduced a chosen number of stage 3 individuals and calculated subsequent transient elasticities. Transient sensitivity is defined by

$$\frac{dn(t+1)}{d\theta^T} = A \frac{dn(t)}{d\theta^T} + (n^T(t) \otimes I_s) \frac{dvec A}{d\theta^T}$$

where  $n$  is a vector of population size in each stage or age at time  $t$ ,  $T$  indicates the transpose operation,  $A$  is the matrix of population transitions defined above,  $\theta$  is the lower level parameter to which sensitivity is being estimated (in our case,  $p_1$ ,  $p_2$  or  $p_3$ ),  $\otimes$  is the Kronecker product defined in Caswell (2001, p. 658),  $I_s$  is an identity matrix of the same dimensions as  $A$ , and  $vec$  is an operator that stacks matrix columns into a column vector. Sensitivities of total population size are obtained by taking the sum of all stage-specific sensitivities. Transient elasticities, corresponding to the transient proportional change of population size to a transient change in a parameter value, are then defined by

$$(N(t))^{-1} \frac{dN(t)}{d\theta^T} \text{diag}[\theta]$$

where  $\text{diag}[x]$  is a matrix with  $x$  on the diagonal and zeros elsewhere.

For a range of values of  $S_j$ ,  $S_a$  and  $F$ , chosen to capture points along a realistic slow-fast continuum of species' life histories, setting the density parameters to  $p_1 = p_2 = p_3 = 0.01$ , we initiated populations for each life history with 50 individuals evenly distributed across the three stages. We then used matrix multiplication to project population dynamics until all life histories reached equilibrium. Because each life history differs in their vital parameters, the rate at which equilibrium is achieved differs, as does the contribution of the various vital rates to this initial growth, and the equilibrium density (see 'Results'). Nevertheless, all life histories attained equilibrium within 100 time steps. We then estimated elasticities of the transient total population size to changes in each of the three density parameters. This captures the effect of changes in the environment leading to increased impact of population density on the vital parameters and is therefore always negative. We then explored the effect of different numbers of arriving individuals (i.e. different levels of influx into a refuge) on the elasticities just described. To allow for comparison across life histories, influx numbers were always measured in reference to equilibrium population size.

## Detailed realistic systems

### Arctic ground squirrels

Karels & Boonstra (2000) provide functional forms relating population numbers  $N$  of arctic ground squirrel to probabilities of summer survival,  $p_s$  ( $p_s(N) = \zeta(0.07 \log(N) + 1.11)$ , where  $\zeta$  indicates the inverse arc-sine transform), winter survival,  $p_w$  ( $p_w(N) = \zeta(-0.95 \log(N) + 1.08)$ ), successful weaning,  $w$  ( $w(N) = \zeta(-0.94 \log(N) + 1.48)$ ), and litter size,  $LS$  ( $LS(N) = -0.38 \log(N) + 2.89$ ), where quantities are standardized to one hectare. Although no distinction between adult and juvenile survival was made, Byrom *et al.* (2000) indicate that juvenile summer survival tends to be lower than adult survival in this population (e.g. in 1992, juvenile 28-day summer survival was 0.477, vs. 0.788 for adults). Subsequent to artificial food supplementation, at all densities, winter survival of arctic ground squirrels increased by  $\sim 0.2$  (Karels & Boonstra, 2000), that is food supply affects the density-independent components of growth. A post-birth census female matrix population model can be constructed from this information using

$$M = \begin{pmatrix} S_j F & S_a F \\ S_j & S_a \end{pmatrix}$$

so that given information on the number of juvenile and adult females at  $t$ , represented by the vector  $n_f(t)$ , the number of juvenile and adult females at  $t+1$ ,  $n_f(t+1)$  can be estimated as  $n_f(t+1) = M n_f(t)$ . Assuming an even sex ratio, adult female survival in this model is defined as  $S_a = p_s(2N_f) \times (p_w(2N_f) + 0.2i)$  where  $N_f$  is the total number of females,  $i$  is an indicator variable defining food availability; juvenile survival is defined as  $S_j = \alpha p_s(2N_f) \times (p_w(2N_f) + 0.2i)$  where the  $\alpha$  coefficient captures the reduction of juvenile versus adult survival; and fertility is defined as  $F = w(2N_f) \times 0.5LS(2N_f)$ . The matrix  $M$  therefore captures the density-dependent population dynamics of arctic ground squirrels. Environmental variation was modelled by simulating a time-series of  $i$  values fluctuating uniformly between one and zero, indicating a good or bad year, respectively. We defined a starting population structure and iterated the model by matrix multiplication for 50 time steps with the simulated values of  $i$  (which was long enough for the population to be fluctuating around its equilibrium). We then introduced between 5 and 70% of the equilibrium population size (taken as  $\sim 1.4$  squirrels  $\text{ha}^{-1}$ ) and explored the consequences on extinction risk using simulation. A simulated population was considered extinct once it fell below a pre-defined extinction boundary of 0.6 individuals  $\text{ha}^{-1}$  (see Lande, Engen & Saether, 2003).

### Wildebeest

Pascual *et al.* (1997) provide functional forms relating juvenile recruitment  $R_j$ , and adult survival  $S_a$ , to population density and rainfall during the dry season (Rain):

$$R_j = \frac{\alpha \frac{\text{Rain}}{N}}{\beta + \frac{\text{Rain}}{N}} \text{ and } S_a = \frac{S_0(\delta + \frac{\text{Rain}}{N}) + \gamma \frac{\text{Rain}}{N}}{\delta + \frac{\text{Rain}}{N}}$$

with  $\alpha = 0.23$ ,  $\beta = 0.000034$ ,  $S_0 = 0.0203$ ,  $\delta = 0.000011$ ,  $\gamma = 0.792$ , indicating the assumption that exploitative competition for resources (that are affected by Rain) drives density-dependent interactions. Pascual *et al.* (1997) also provide age-specific rates of female births per adult female, which are 0.53 for 4 year olds, and one for females  $\geq 5$  years old. As juvenile recruitment includes survival to the first year, together, these define a post-birth census matrix population model:

$$M = \begin{pmatrix} 0 & 0 & 0.53S_a & S_a \\ R_j & 0 & 0 & 0 \\ 0 & S_a & 0 & 0 \\ 0 & 0 & S_a & 0 \\ 0 & 0 & 0 & S_a \end{pmatrix}$$

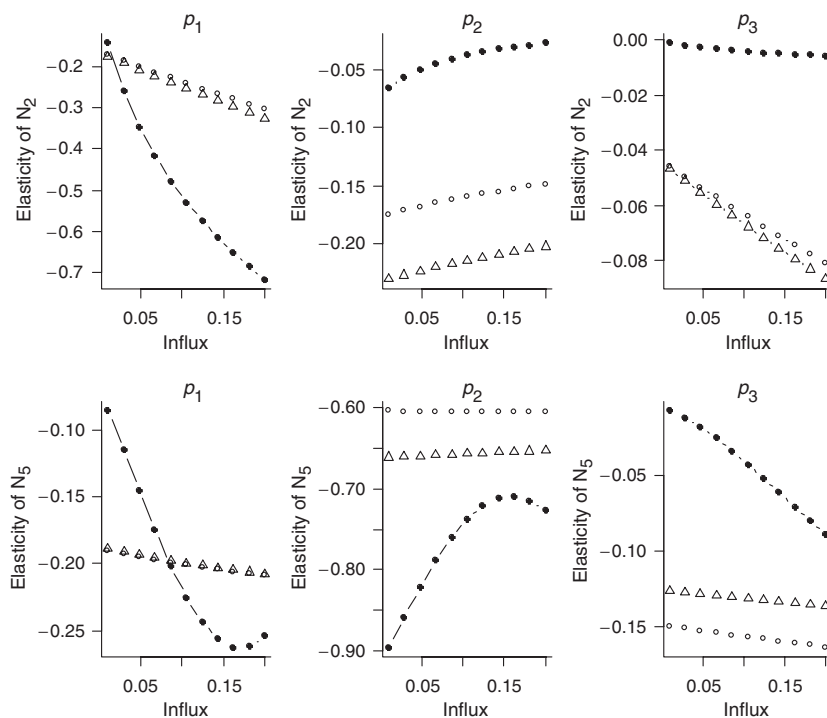
We simulated the corresponding stochastic population dynamics by assuming that rainfall varied from year to year and followed a normal distribution with mean 150 and standard deviation of 40, mimicking levels indicated to dominate between 1950 and 1990 (Pascual *et al.*, 1997). We

defined a starting population structure and iterated the model to ensure that populations were fluctuating around an equilibrium. We then introduced a number of adults equal to between 2 and 110% of the extant population size to explore the consequences for extinction risk, using an extinction threshold of 1000 individuals.

## Results

### Transient dynamics in a simplified system

For all life-history types considered, an influx leads to overcompensatory fluctuations around the equilibrium (Fig. 1). The magnitude of these fluctuations is larger in the life history with high reproduction and low survival, and smaller for those with low reproduction and high survival. At the second time step following influx, all life histories are below equilibrium. At time step 5, life histories are above their equilibrium. Because increases in the magnitude of density dependence always decrease population size, transient elasticities of  $N$  to changes in the density-dependent parameters,  $p_1$ ,  $p_2$  or  $p_3$ , are always negative (Fig. 2). The diminished population sizes at time step 2 will therefore be further reduced by any increase in the density-dependent parameters. The same holds at time step 5, when population size is above equilibrium. Consequently, increases in density-



**Figure 2** Transient elasticity at  $t=2$  (first row) and  $t=5$  (second row) of total population size to (1)  $p_1$ , a parameter governing the density-dependent effect on fertility,  $F$ ; (2)  $p_2$ , a parameter governing the density-dependent effect on juvenile survival,  $S_j$ , and (3)  $p_3$ , a parameter governing the density-dependent effect on adult survival,  $S_a$ , for population influxes of 5–20% of the equilibrium population size (x axis, units are in proportion to equilibrium population size). The starting population is at equilibrium. Three different life-history types are considered, (1) species with low adult and juvenile survival and high fertility ( $S_j = S_a = 0.2$ ,  $F = 25$ , filled points); (2) species with low juvenile survival, high adult survival, and low fertility ( $S_j = 0.6$ ,  $S_a = 0.8$ ,  $F = 3$ , empty points); (3) species with high juvenile survival, high adult survival, and low fertility ( $S_j = S_a = 0.8$ ,  $F = 3$ , triangles).

dependent competition following influx reduce transient population size both during periods where population size is below equilibrium and above the equilibrium, a result that is due to the effects of changes in  $p_1$ ,  $p_2$  or  $p_3$  on population structure.

The three different life histories show different patterns of changes in elasticity with changes in influx size. If the force of density dependence on fertility increases, the larger the influx, the more transient population size is reduced ( $p_1$ , Fig. 2). However, after five time steps, the effect on high survival, low-fertility life histories (open circles and triangles) only varies slightly with influx size, and the direction of the effect on low survival, high-fertility life histories (filled circles) even changes. This indicates that if populations survive through the initial negative effects on population size (which are worse for larger influxes), higher influx sizes may eventually increase population sizes, if they are sufficient to counterweight the negative early effect of amplified density dependence on total population size. This effect is more important for the high-fertility life history as it is most affected by density dependence acting on fertility.

If density dependence acting on juvenile survival intensifies ( $p_2$ , Fig. 2), an influx of individuals counterweights the negative effects of increasing density dependence for all three life-history types for population size at  $t = 2$  and an influx of individuals has a net positive effect on the total population size as it is sufficient to swamp the negative effects of increased density-dependent juvenile survival. However, at  $t = 5$ , after an initial increase, the high-fertility life history (open circles) again experiences negative effects of a greater number of arriving individuals, as the number of arriving individuals is so great that no new offspring successfully survives to the age at first reproduction.

For the effect of an intensification of density dependence acting on adult survival ( $p_3$ , Fig. 2), influx of individuals does not much affect the transient population size of the high-fertility life history at  $t = 2$ ; the other two life histories show increasingly severe effects with increasing influx size. At  $t = 5$ , the high-fertility life history also shows this pattern. The time lag before the negative effect following an influx is observed in the high fertility life history because the negative effect will only manifest itself following reproduction in the new higher-density context.

### Detailed realistic systems

For arctic ground squirrels, combinations of bad years and high densities can drive adult survival to very low levels, and also affect fertility (Fig. 3a). Consequently, an influx of individuals does increase the risk of extinction for ground squirrel populations (Fig. 3b), and this risk depends on a threshold number of individuals arriving (Fig. 3c). If extinction occurs, it is in the time step immediately following introduction and coincides with a bad year. For the longer-lived wildebeest, with the environmental conditions described, the equilibrium distribution of population size is very high, and even at high densities in conditions of poor rainfall, adult survival does not fall below  $\sim 0.7$  (Fig. 4a).

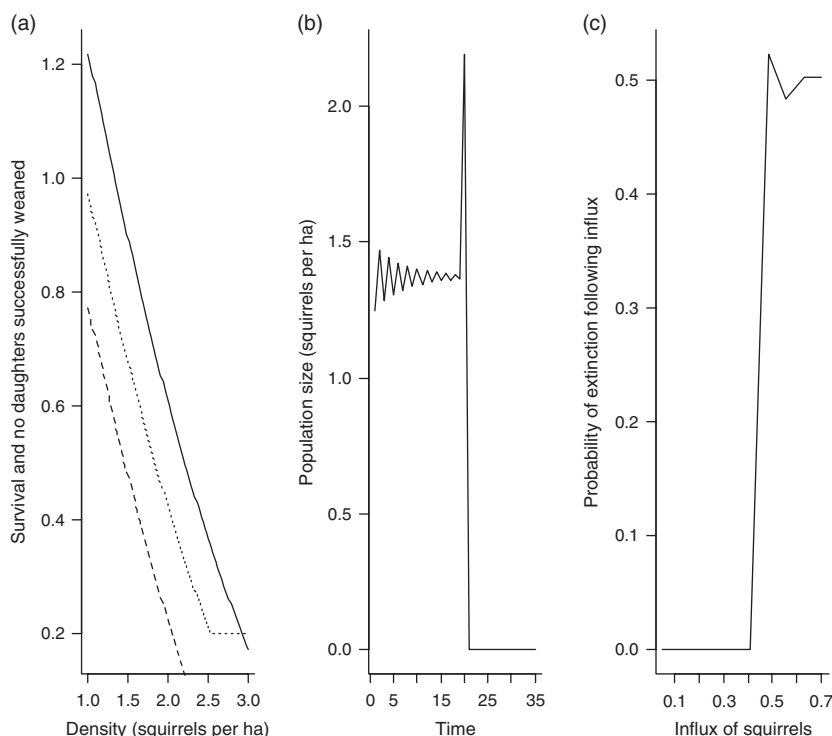
Consequently, no influx of individuals can sufficiently perturb the population to yield extinction (a range of influx sizes from 2–110% of population size was tested). Following influx, in a very short period, populations rapidly return to dynamics that are observed in the absence of perturbations. Thus, wildebeest dynamics in a refuge are relatively insensitive to influx numbers (Fig. 4b).

### Discussion

Most of the extensive work on habitat loss and fragmentation (reviewed by Fahrig, 2003) assumes populations are at equilibrium. Here we focused on transient dynamics, increasingly recognized as being important for understanding ecological systems (Neubert & Caswell, 1997; Hastings, 2004). Both the population's structure and the way in which density dependence operates can have strong implications for outcomes of animals arriving in refuges. In relatively long-lived wildebeest with large population sizes, the threat to populations is extremely small, but with shorter lived species such as arctic ground squirrels, where there is no long-lived stage to buffer the population through adverse conditions, the risk can be higher. If extinction occurs, it is caused by the large transient reaction (Caswell & Neubert, 2005) immediately following introduction.

Analysis of transient elasticities following an influx of individuals into a refuge indicates that effects can be both non-linear and dependent on the time step at which they are measured. Nevertheless, they are negative in most situations for the density-regulated models that we considered. Comparison across life histories indicates that shorter-lived life histories are more at risk following influx into a refuge when density dependence acts on fertility or juvenile survival if it is sufficient to curtail recruitment entirely (Fig. 2). A range of small mammals (other rodents, etc.) may fall into this category. In contrast, Koons *et al.* (2005) found that longer-lived organisms always experienced larger magnitudes of transient reactions following perturbations to density-independent vital rates and population structure. Our patterns in transient elasticities under different life histories following an introduction of individuals into a refuge differ because of the dual transient effects of density-dependent feedback on the vital rates and unstable age structure in our models. Results indicate that refuge populations of longer-lived organisms will be threatened following population influx if density dependence acts on survival. This might have conservation implications for species like blue petrels *Halo-baena caerulea* where survival is density dependent and tied to environmental fluctuations (Barbraud & Weimerskirch, 2003). Blue petrel populations also do not benefit from the protective role of large population sizes that characterize Serengeti wildebeest, which may also be the case for other ungulates that experience density-dependent survival, for example Soay sheep (Coulson *et al.*, 2001). More detailed exploration of transient fluctuations of age structure will deepen the understanding of when populations will be at risk.

We considered a relatively simple situation where density dependence had monotonic effects on vital rates. However,

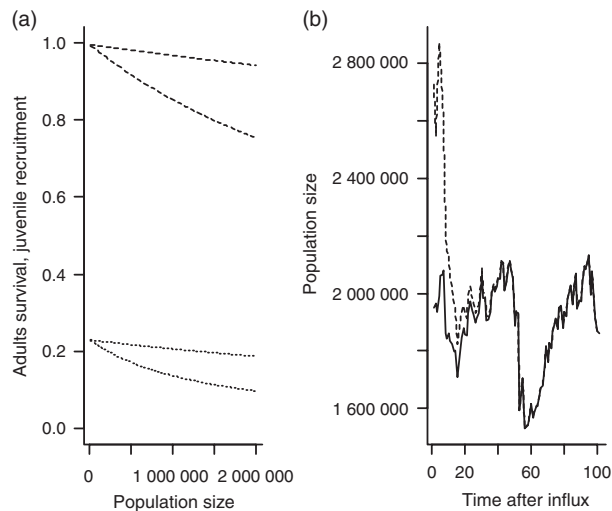


**Figure 3** (a) Arctic ground squirrel winter survival for 'good' (dotted line) and 'bad' (dashed line) conditions; and number of females successfully weaned (solid line), taken across a range of densities, from parameters in Karels & Boonstra (2000). 'Bad conditions' correspond to no food supplement and 'good' to the gains in survival ( $\sim 0.2$ ) that resulted from artificially supplied food supplements. (b) Corresponding stochastic population dynamics of squirrel numbers per hectare, where conditions fluctuate randomly between 'good' and 'bad'. In this example, at  $t=20$ ,  $0.8$  individuals  $\text{ha}^{-1}$  were introduced into the population and this was sufficient to drive the population below the extinction threshold ( $0.6 \text{ ha}^{-1}$ ). (c) The simulation was repeated 5000 times for increasing influx magnitudes (x-axis, units are in proportion to equilibrium population size). Risk of extinction in the time-step immediately following introduction goes to a maximum of  $\sim 0.5$  when there is an influx of  $\sim 40\%$  of the current population density. Half the time the food environment is 'good' and half the time it is 'bad' and only in 'bad' environments does an influx of immigrants lead to extinction.

catastrophic declines can be caused by factors that have density-dependent feedbacks, particularly disease (Wilcox & Elder, 2003), and epidemics occurring once a population has exceeded a threshold size can dramatically reduce the size of a population (Grenfell & Dobson, 1995). In such contexts, low-density populations may be a valuable resource in metapopulation persistence (Wilcox & Elder, 2003), which may be lost by an influx of individuals fleeing a catastrophe.

Another complexity not considered is that of interactions between different trophic levels. Predators typically have larger ranges than their prey and consequently may be more likely to find a refuge following a sudden catastrophe such as a fire, putting prey populations at risk (Holt & Hochberg, 2001). Certain types of prey, such as obligate cooperative breeders, may be more vulnerable to increases in predator numbers than others (Courchamp, Grenfell & Clutton-Brock, 2000). Prey may also be more vulnerable while at higher densities both through being easier to locate, and by supporting larger predator populations. This recognized problem has prompted a drive to create 'low density refuges' for endangered bird species (Sinclair *et al.*, 1998). Although

many models assume density dependence is negligible in predators (Neubert, Klanjscek & Caswell, 2004), empirical evidence suggests such interactions are a non-negligible component of dynamics (Skalski & Gilliam, 2001), so that predators also may be at risk following population influxes (Holt & Hochberg, 2001). Additionally, increased prey density may increase competition between carnivore species via behavioural responses (Creel, 2001) so that increased prey numbers can put predator populations at risk. For example, release from rinderpest led to a rise in wildebeest numbers in the Serengeti and corresponding growth in lion and hyena populations. However, this increased competition caused wild dog populations to decline over the same period, leaving them vulnerable to other stochastic forces such as disease, eventually causing their local extinction (Ginsberg *et al.*, 1995). Predator search efficiency may also decline with increasing predator numbers as prey become more shy, or collectively more able to evade predators perhaps as a consequence of heightened awareness (Krause, 1993) or due to the confusion effect (Krakauer, 1995). Modelling indicates that the introduction of more individuals can tip communities from one stable state to another



**Figure 4** (a) Survival (dashed line) and recruitment (dotted line) for the best (300) and worst (50) conditions of rainfall during the dry season on the Serengeti, across a range of densities following functional forms and parameters provided in Pascual *et al.* (1997) and the methods. (b) Corresponding stochastic population dynamics of wildebeest from time step 500 to time step 600 where rain fluctuates randomly following a normal distribution with mean 150 and standard deviation 40 (wildebeest yearly total population size indicated by a solid line); and population dynamics following introduction of 50% of the population at time step 500 into an identical environmental sequence of rain (wildebeest yearly total population size indicated by a dashed line). The population initially diverges and then rapidly returns to the previous trajectory without ever going below the extinction threshold.

(Sinclair & Pech, 1996), with the risk of ending up in stable states where only a few species persist. Another complication not addressed here is the potential risk that arises through local adaptation. If immigrants are less well-adapted to the habitat that they invade, then by breeding with residents they may launch insidious decline in the general health of the population (Tallmon, Luikart & Waples, 2004).

The ideas discussed here are applicable to all types of habitat loss, from natural causes through to anthropogenic causes like deforestation, wildfires or development, and all speeds of population influxes. To further understanding, effects of crowding could be explored both experimentally and in natural systems. Ponds and lakes that dry out provide an ideal system where crowding may be induced as available habitat shrinks. Indeed, catastrophic outbreaks of disease and cannibalism recorded in aquatic populations (Griffiths, 1997) are prime examples of the extreme density-dependent responses likely to pose a threat to populations following a population influx. Animal translocations, which in several areas have become standard practice as a means of reducing the impact of planned development or habitat destruction, are another interesting source of data. Many translocations are monitored with scientific rigour, particularly if the species of concern is being reintroduced to an unoccupied

habitat or following a captive breeding programme and here the emphasis of monitoring is on the survival of the relocated animals (Towns & Ferreira, 2001). However, most translocations initiated as a result of intended development are rather less well-planned, and even less well-monitored (Fischer & Lindenmayer, 2000). Often animals are moved to occupied, sometimes adjacent habitat (which might lead to higher levels of influx than the process of natural immigration following a disturbance). Many of these translocations have been shown to be ineffective due to high mortality of the introduced animals (Fischer & Lindenmayer, 2000; Hughes *et al.*, 2003). From the interactions described above, the consequences of such translocations could be much more damaging. Theoretical work indicates that in the presence of delayed density dependence, repeated re-introductions may be particularly problematic (Holt, 2002). We did not assess effects of repeated re-introductions on transient dynamics and extinction risk where density dependence is immediate, but this indicates further study is warranted. Evaluation and monitoring of translocation programs would provide a valuable testing ground for the mechanisms we have proposed.

A final consideration is that even where crowding is not a direct threat to population persistence, crowding may lead to misinterpretations of population status. It has been shown that following fragmentation, there is a period of 'faunal relaxation' during which species diversity is higher than the eventual equilibrium level (Robinson, 1999), leading to the concept of an 'extinction debt' (Tilman *et al.*, 1994; Brooks, Pimm & Oyugi, 1999). A similar process could occur within species. This has not received much attention (but see Hagan *et al.*, 1996; Ovaskainen & Hanski, 2003), but has important implications. When interpreting population estimates it is important to know whether a population may be 'crowded' following a perturbation. If relaxation is slow, the age-structure and corresponding transient dynamics of the population may more accurately reflect true population health.

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