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Evolution of dispersal in American pika (*Ochotona princeps*) metapopulations

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ABSTRACT

Question: How might global climate change affect American pika (*Ochotona princeps*) metapopulation dynamics in the Great Basin, and how would such effects impact evolutionary dynamics of dispersal?

Mathematical methods: A structured, semi-discrete, mechanistic metapopulation model in which patch age is the structuring variable. We apply adaptive dynamics for the evolutionary analysis and derive an invasion fitness proxy for this model setting.

Key assumptions: Global climate change potentially alters the probability of patch extinction, dispersal costs, mortality, and fecundity. Births and immigration occur at discrete points in time. Deaths and emigration occur continuously over time. We model 'average' patch dynamics.

Results: Potentially viable metapopulations nevertheless can be destined for extinction via evolutionary suicide driven by climatic forcing. Specifically, selection can drive down dispersal rates in viable metapopulations, degrading colonization rates and increasing extinction rates to the point where the metapopulation crashes.

Conclusions: Exclusive reliance on ecological dynamics without this evolutionary perspective would miss the phenomenon identified here. This result arises in realistic ranges of parameters and therefore generates a testable hypothesis with potential applications to long-term metapopulation sustainability.

Keywords: adaptive dynamics, climate change, dispersal, evolutionary suicide, metapopulation, *Ochotona princeps*.

1. INTRODUCTION

American pikas (*Ochotona princeps*) comprise five subspecies of small, talus-dwelling lagomorphs distributed primarily in the Rocky Mountains and Cascade ranges in the United States and southern Canada, the Sierra Nevada, and ranges in the Great Basin into central Utah and eastern Washington in the USA (Smith and Weston, 1990; Hafner and Smith, 2010). This species most commonly inhabits talus fields at elevations >2500 m in the Sierra

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Nevada, Great Basin and southern Rocky Mountains, and has done so from the Pleistocene until recent times (Smith and Weston, 1990; Grayson, 2005). The limitation of the pikas' range to high elevation appears to be due in large part to physiological constraints. Smith (1974b) performed a study of the (in)ability of pika physiology to handle warm temperatures at a site east of the Sierra Nevada crest near the ghost mining town of Bodie, California. He observed that caged pikas exposed to direct sunlight died when ambient air temperatures in the shade ranged between only 25.5° and 29.4°C (black bulb temperatures of 31.4°C), a discovery that has prompted speculation that global climate change, among other anthropogenic factors, represents a threat to American pikas in the Great Basin (Beever *et al.*, 2003).

The above-mentioned hypothesis is supported by a number of lines of evidence. Paleontological evidence suggests that, throughout the Great Basin, the lower elevation limit of American pika populations has risen an average of about 400 m since the Pleistocene (Grayson, 2005), presumably due at least in part to a warming climate in that interval. As a result, many isolated populations, especially in the eastern and southern parts of the prehistoric range, have gone extinct (Beever *et al.*, 2003; Grayson, 2005). Precisely when these extinctions occurred remains unclear. However, small mammal populations in the Sierra Nevada – essentially the western wall of the Great Basin – have generally shifted their elevation limits upward over the last 100 years, and these alterations are not due to anthropogenic changes in land use (Moritz *et al.*, 2008).

Nevertheless, two other lines of evidence tend to counter the notion that American pikas in the Great Basin are currently declining due to global climate change. First, although Smith (1974b) documented the inability of pika physiology to handle even mildly warm temperatures, he points out that normally these animals would have avoided hyperthermia by seeking refuge in the talus. In addition, Bodie pikas have acquired other behavioural adaptations to their comparatively warm environment, in particular by restricting their above-talus activities during the day and becoming more openly active overnight, compared with pikas at higher elevations in the nearby Sierra Nevada (Smith, 1974b). Indeed, summer temperatures at Bodie routinely exceed the temperatures Smith found to be lethal, yet Bodie has supported a pika metapopulation for over 100 years (Severaid, 1955; Smith, 1974a, 1974b, 1978, 1980; Nagy, 1996; Peacock and Smith, 1997; Moilanen *et al.*, 1998; Clinchy *et al.*, 2002).

The second line of contradictory evidence is the recent discovery by Millar and Westfall (2010a) of robust pika populations in several low-elevation sites – many even lower than Bodie – in the western Great Basin (see also Wolf, 2010 and Millar and Westfall, 2010b for further commentary). Consistent with this discovery is the observation of a large, low-elevation pika population in Craters of the Moon National Park, Idaho, USA (Rodhouse *et al.*, 2010). Although this site is physically quite distinct from the southwestern margin of the Great Basin, talus characteristics in both areas appear to provide refuges from warm summer temperatures, allowing behavioural adaptations to avoid hyperthermia (Millar and Westfall, 2010a; Rodhouse *et al.*, 2010).

Given this contradictory evidence, the precise effects of global climate change on American pika populations in the Great Basin and adjacent Sierra Nevada now and in the future remain an open question. The nature and magnitude of the impact on pika populations from global climate change critically depends on the animal's ability to adapt to changes in climate. Smith (1974b) shows directly, with circumstantial support from Millar and Westfall (2010a) and Rodhouse *et al.* (2010), that pikas can adapt behaviourally to relatively warm climates. Alteration of diurnal activity patterns marks one such adaptation.

Other hypothesized adaptations include changes in dispersal behaviour. Throughout their range, pikas appear to be generally philopatric, and in the Great Basin and Sierra

Nevada, natal dispersal in pikas is rare on ecological timescales (Severaid, 1955; Nagy, 1996; Peacock and Smith, 1997). However, the Bodie population presents a very interesting special case. On the one hand, the heat typical of Bodie appears to make it more difficult for pikas to move among patches than at higher elevations, increasing the direct costs of dispersal (Smith, 1974b). On the other hand, pikas at Bodie establish territories on ore dumps, which replace the natural talus habitats used in natural settings. With only a few exceptions, these ore dumps are small – typically harbouring a maximum number of territories less than 10 – and physically separated from other suitable habitat. Therefore, Bodie has long been recognized as a metapopulation (Severaid, 1955; Smith, 1974a, 1974b, 1980; Nagy, 1996; Peacock and Smith, 1997; Smith and Gilpin, 1997). Since patch sizes, and thus local populations, are small, however, a significant number of local populations go extinct from demographic stochasticity. The relatively high patch extinction rate with close spacing of most patches alters the relative costs and benefits of dispersal and philopatry in the favour of dispersal. Given time and sufficient genetic variation, mathematical models predict that the Bodie pikas will not only disperse more and more even when dispersal's direct costs are very high, the metapopulation will become decreasingly likely to go extinct, all else being equal (Nagy, 1996).

Global climate change, however, represents a wild card in this evolutionary scenario. The potential effects of a changing climate on costs and benefits of dispersal remain essentially unexplored. Yet dispersal behaviour largely determines the persistence of metapopulations and other spatial population structures relevant to pikas in the western Great Basin and Sierra Nevada (Levins, 1969, 1970). Here we initiate this exploration by formulating and analysing a model of dispersal in metapopulations like the Bodie pikas. Our model is defined in semi-discrete time, with continuous dynamics between breeding seasons connected with discrete breeding events. Catastrophes, which include any mechanism causing local population extinction, may wipe out local populations leaving patches habitable for immigrants coming from other patches via a dispersal pool. As our aim is to study evolution of a behavioural trait, namely dispersal, we apply the adaptive dynamics framework (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998) and use the metapopulation reproduction ratio (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) as a fitness proxy in our metapopulation model.

Our primary aim in this study is to explore the possible effects global climate change may have on pika population dynamics and evolution of dispersal in this species; more precisely we ask, what are the possible scenarios impacting the evolution of dispersal? We identify global climate change as a change in model parameters (e.g. catastrophes, dispersal cost, mortality, and survival rate) and analyse how these variations affect evolutionarily stable dispersal strategies in a metapopulation. We use this modelling framework to evaluate which parameters are likely to have the greatest impact on viability and selection for dispersal in pika metapopulations. We see this as an initial investigation to help organize research priorities.

2. MODEL AND METHODS

2.1. Metapopulations

The metapopulation concept was introduced by Levins (1969). In general, a metapopulation is a collection of local populations living in distinct habitat patches that are connected by dispersal. Catastrophic events may cause patch extinction, but dispersers from extant patches may recolonize those extinct patches. Levins (1969) showed that the metapopulations persist only if the recolonization rate exceeds the extinction rate. Hence, dispersal among patches is a key feature in the survival of a metapopulation.

Levins' metapopulation model is unstructured in the sense that it tracks only the dynamics of occupied and unoccupied patches, not dynamics on patches. Therefore, the Levins approach is an awkward tool to apply to the evolution of life-history traits like dispersal. For this we need more specific mechanistic models that operate at the individual level. Here we propose a structured metapopulation model (Metz and Gyllenberg, 2001; Gyllenberg and Metz, 2001; Parvinen, 2006) with infinitely many habitat patches and realistic local population dynamics. Before going deeply into the metapopulation dynamics, we first describe local dynamics at the individual level.

2.2. Local semi-discrete population dynamics

We assume that pikas experience a sequence of 'phases' or seasons throughout the year in which population dynamic forces vary. Time within a year is measured by $t \in [0, 1]$. A population census occurs at the beginning of each year ($t = 0$), weaning of the young occurs at time τ_1, after which the juvenile may emigrate until $t = \tau_2$. All dispersers enter a global dispersal pool and are randomly distributed among patches at a discrete point in time, τ_2. After immigration, local (within-patch) dynamics continue as before but without emigration. The time points mark the boundaries between behavioural 'seasons', so $0 < \tau_1 < \tau_2 < 1$ (Fig. 1). Within each season, pikas experience a more-or-less fixed constellation of forces, but the set of forces changes at discrete points of time. Within-season dynamics are governed by a system of differential equations, while another set of dynamical equations describing discrete (instant) events connects different seasons (Geritz and Kisdi, 2004; see also Eskola and Geritz, 2007; Eskola and Parvinen, 2007, 2010). Following Ghosh and Pugliese (2004), Pachepsky *et al.* (2008), and Singh and Nisbet (2007), we use the name 'semi-discrete' for such models.

Habitat patches are identical and each contains a static number, K, of potential territories. Let $A(t)$ denote the density of adult territory owners on a patch in a given year at time $t \in [0, 1]$. Over winter (from time 0 to τ_1), adults suffer a constant mortality rate, and patches can be completely depopulated in some catastrophic way over winter. Offspring are

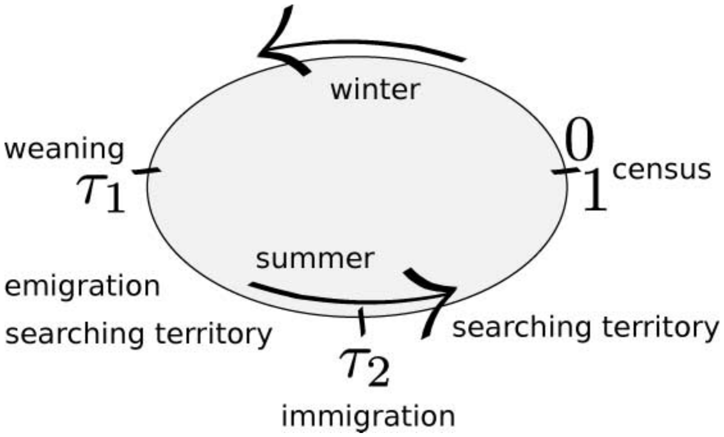

Fig. 1. Idealized life cycle of pikas. Time $t = 0$ is labelled 'census'. Weaning occurs at τ_1, when emigration takes place until the immigration event at time τ_2.

born and weaned in spring (at time τ_1), at which time we refer to them as juveniles. Throughout the next season (summer), juveniles compete for territories. The density of unestablished juveniles (without a territory) at time $t \geq \tau_1$ is denoted $J(t)$, while the density of established juveniles (with a territory) is denoted $B(t)$. In early summer, unestablished juveniles may emigrate from patches and enter a 'dispersal pool'. Let $D(t)$ be the density (measured per patch) of dispersers in this pool. At time τ_2 emigration stops, and juveniles in the dispersal pool immigrate into the patches, immediately entering back into competition for territories.

Although assuming separation of emigration and immigration into discrete seasons or events may seem biologically unrealistic, we model dispersal this way mainly for technical reasons: for dispersers, the dispersal pool size at time τ_2 becomes a unique 'birth state' allowing calculation of fitness using the metapopulation reproduction ratio (Metz and Gyllenberg, 2001). This assumption is unlikely to have a major impact on either population or evolutionary dynamics.

We choose to mark the beginning of each year with an autumn census because such a census has been performed at Bodie off-and-on since the 1970s (Smith, 1980; Peacock and Smith, 1997; Moilanen *et al.*, 1998; Clinchy *et al.*, 2002). In the field, this census focuses on the haypiles characteristic of this species; pikas survive winter by feeding on hay collected in summer. These haypiles also serve as territorial markers. Since pikas without territories, and therefore without a haypile, cannot survive winter, we assume that at the time of the census (at time 1) only pikas with territories survive. At the census, juveniles who have established themselves on a territory become adults. Therefore, $J(t), B(t) \equiv 0$ for all time $t \in [0, \tau_1)$. We now describe the dynamics of each phase in turn.

2.2.1. *Winter and reproduction* ($0 \leq t < \tau_1$)

Since only juveniles established on territories become adults at the time of the autumn census ($t = 1$),

$$A(t = 0 \text{ for coming year}) = A(1) + B(1).$$

Over winter ($t \in (0, \tau_1]$) all adults suffer a constant per capita mortality rate; therefore,

$$A(\tau_1) = (1 - \mu_w)A(0),$$

where $\mu_w \in [0, 1)$. (We assume $\mu_w < 1$ to avoid a trivial model.) We assume that weaning occurs precisely at time τ_1 for all juveniles. Thus, in our model 'reproduction' includes both

Table 1. Different types of individuals in the model

Notation	Definition
A	Adult
J	Juvenile without a territory
B	Juvenile with a territory
F	Emigrated juveniles
D	Juveniles in dispersal pool

Note: The same notation is used to describe the local population density of the respective type.

birth and survival to weaning; newborn pikas are not explicitly modelled. The number of juveniles at the beginning of emigration is then

$$J(\tau_1) = f(A(\tau_1)),$$

where f is an unspecified fecundity function of A. In the numerical analysis we have used function $f(A) = \frac{b}{2}A$, where b describes mean reproduction per pika pair.

2.2.2. *Early summer and emigration* ($\tau_1 \leq t < \tau_2$)

During early summer juveniles on patches both search for empty territories and challenge adults and other juveniles for territories. Some juveniles emigrate from their natal patch into a dispersal pool from which they will later immigrate to another patch. At the beginning of summer no juveniles are yet established on territories, so

$$B(\tau_1) = 0.$$

Our model of early summer dynamics then takes the following form:

$$\begin{cases} \dot{A} = -(\mu_A A + \gamma_{JA} JA), \\ \dot{J} = -(\mu_J J + (\gamma_{AJ} + \gamma_{JA}) JA + (\gamma_{JB} + \gamma_{BJ}) JB + \beta JE + eJ), \\ \dot{B} = \gamma_{JA} JA + \beta JE + \gamma_{JB} JB - \gamma_{JB} JB - \mu_B B, \end{cases} \tag{1}$$

where $E = K - A - B$ is the density of empty territories, and e describes a juvenile's propensity to disperse. Philopatric, unestablished juveniles settle on vacant territories at rate β. Pikas die with per capita mortality rates described by parameters of the form μ_x, with $x \in \{A, J, B\}$ referring to adult, unestablished juvenile and established juvenile, respectively. All parameters γ refer to attempts by juveniles to establish themselves on territories. Specifically, γ_{JA} is the rate at which unestablished juveniles successfully challenge an adult for the adult's territory, followed by the death of the adult. On the other hand, γ_{AJ} is the rate at which such challenges are unsuccessful (with the subsequent death of the challenging juvenile). Similarly, γ_{JB} and γ_{BJ} are rates at which unestablished juveniles either successfully or unsuccessfully attempt to unseat an established juvenile. Later analysis will be simplified if we define parameters γ as follows:

$$\begin{aligned} \gamma_{JA} &= \hat{\gamma}_{JA} p_1 \\ \gamma_{AJ} &= \hat{\gamma}_{JA}(1 - p_1) \\ \gamma_{JB} &= \hat{\gamma}_{JB} p_2 \\ \gamma_{BJ} &= \hat{\gamma}_{JB}(1 - p_2), \end{aligned} \tag{2}$$

where $\hat{\gamma}_{JA}$ and $\hat{\gamma}_{JB}$ are the rates at which juveniles challenge territory holders, and p_i is the proportion of times this challenge is successful. Note that a successful territorial challenge by an unestablished juvenile on an established one results in no net change in B, hence the terms $\pm\gamma_{JB} JB$ in the third equation of system (1).

To model dispersers, let $F(t)$ be the amount of juveniles emigrating from a patch between τ_1 and t. Emigration into the dispersal pool, where the dispersers suffer a per capita mortality rate μ_J, in early summer is modelled, then, by the following differential equation:

$$\dot{F} = eJ - \mu_J F, \qquad F(\tau_1) = 0.$$

Let π be the probability that an emigrating individual survives the transition from the local population into the dispersal pool. In addition, juveniles in the dispersal pool experience the same natural mortality μ_J as juveniles in local populations. The quantity $1 - \pi$ can be thought of as the cost of dispersal. At time $t = \tau_2$, emigration stops. Thus, at time τ_2,

$$\hat{F} = \pi F(\tau_2) \tag{3}$$

dispersers from the patch survive.

2.2.3. *Late summer and immigration* ($\tau_2 \leq t < 1$)

At time $t = \tau_2$ dispersers in the dispersal pool are instantly distributed to all patches. Immigration happens randomly and does not depend on patch properties such as the local population size. Immigrants enter patches as unestablished juveniles and immediately begin competing for territories. Thus, late summer dynamics are described by the following model:

$$\begin{cases} \dot{A} = -(\mu_A A + \gamma_{JA} JA), \\ \dot{J} = -(\mu_J J + (\gamma_{AJ} + \gamma_{JA}) JA + (\gamma_{JB} + \gamma_{BJ}) JB + \beta JE), \\ \dot{B} = \gamma_{JA} JA + \beta JE + \gamma_{JB} JB - \gamma_{JB} JB - \mu_B B, \end{cases} \tag{4}$$

with the initial value $J(\tau_2) = J(\tau_2 -) + \hat{D}$, where $\hat{D}$ is the average amount of dispersers $\hat{F}$ over all patches, i.e. the size of the dispersal pool. Note that $\hat{F}$ varies in different patches, and therefore is, in general, unequal to $\hat{D}$ (equation 5). Note also that unlike $J(t)$, the densities $A(t)$ and $B(t)$ are continuous at time τ_2 and that the dynamics remain unchanged but the negative emigration term for $\dot{J}$ is erased.

Parameter notations and their default values used in numerical analysis are summarized in Table 2.

2.3. Metapopulation dynamics

On the metapopulation level, we are interested in the distribution of local population sizes. Although this is essentially a book-keeping task, it can be technically rather demanding. However, the problem of finding metapopulation-dynamical equilibria is clarified if we use patch 'age' as a structuring variable.

2.3.1. *Metapopulation-dynamical equilibria*

Let ξ denote the 'age' of the patch, i.e. the number of years (time steps) since a catastrophe (extinction) last occurred in the patch. A patch with age 0 has just gone extinct. Therefore, it remains empty during early summer. At time τ_2 it will receive some amount of immigrants, which generally varies by year because the dispersal pool size varies by year. However, if we assume that the dispersal pool size is constant, say at $\hat{D}$, then all patches of age 0 will have the same within-season population sizes. A patch of age 0 becomes a patch of age 1 at the next census, if it does not go extinct during the next winter. Since the initial conditions and dynamics of all patches of age 1 are identical, they will have the same within-season population sizes, and so on. This reasoning can be continued to all ages, and thus $\hat{D}$ and the patch age ξ uniquely determine the local population sizes $A(\xi, t, \hat{D})$, $B(\xi, t, \hat{D})$ and $J(\xi, t, \hat{D})$ for all $t \in (0, 1]$. The same argument applies to the number of emigrants, $\hat{F}(\xi, \hat{D})$, from a patch of age ξ (equation 3).

Table 2. Parameter notation and their default values

Definition	Notation	Default value
Fecundity	b	3
Winter mortality	μ_w	0.05
Constant catastrophe rate	μ_c	0.01
Catastrophe rate in full patch	μ_K	0.005
Catastrophe rate in empty patch	μ_0	0.5
Steepness in catastrophe function	z	10
Seasonal mortality rate of:		
adults	μ_A	0.2
unestablished juveniles	μ_J	0.5
established juveniles	μ_B	0.4
Rate of territory challenges:		
juvenile vs. adult	$\hat{\gamma}_{JA}$	0.2
juvenile vs. juvenile	$\hat{\gamma}_{JB}$	0.4
Proportion of successful challenges:		
juvenile vs. adult	p_1	0.1
juvenile vs. juvenile	p_2	0.2
Rate of obtaining an empty territory	β	1
Dispersal survival probability	π	0.9
Carrying capacity, territories	K	1
Starting time of early summer season	τ_1	0.4
Starting time of late summer season	τ_2	0.7

Based on the above reasoning, a fixed dispersal pool of size $\hat{D}$ determines a quasi-equilibrium for the metapopulation model. To find the actual metapopulation-dynamical equilibria, we need to find such dispersal pool sizes that remain constant in a quasi-equilibrium. In other words, $\hat{D}$ at time τ_2 has to satisfy the condition,

$$\hat{D} = \sum_{\xi=0}^{\infty} \hat{F}(\xi, \hat{D}) p(\xi, \hat{D}). \tag{5}$$

The frequency distribution $p(\xi, \hat{D})$ of patches of age ξ satisfies the conditions

$$\sum_{\xi=0}^{\infty} p(\xi, \hat{D}) \equiv 1, \qquad p(\xi+1, \hat{D}) = (1 - \mu_c(A(\xi+1, 0, \hat{D}))) p(\xi, \hat{D}). \tag{6}$$

If the extinction rate μ_c is constant, i.e. does not depend on the local population size, we obtain $p(\xi) = \mu_c(1-\mu_c)^{\xi}$ from (6). This is also the probability that a patch survives ξ years and is then hit by a catastrophe. More realistically, one can consider extinction rates that are decreasing functions of the local population size at the time of census, A. This Allee effect can result, for example, from a predator being able to attack unnoticed and extinguish a small population, but being more likely to be detected in a large population. In particular, we apply the function suggested by Gyllenberg *et al.* (2002):

$$\mu_c(A) = \mu_0 \left[1 - \left(1 - \frac{\mu_K}{\mu_0} \right) \frac{1 - \exp(-zA/K)}{1 - \exp(-z)} \right], \tag{7}$$

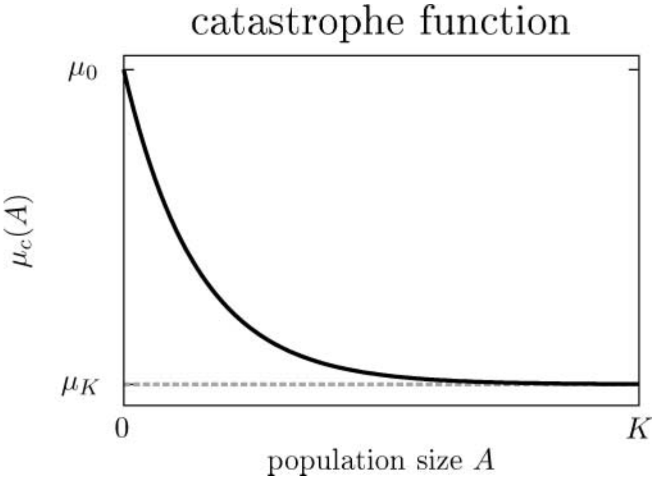

Fig. 2. Catastrophe rate as a function of local population size A in a patch.

where parameters μ_0 and μ_K describe the extinction rate in empty and full patches, respectively (see Fig. 2 and Table 2).

The metapopulation equilibrium condition (5) can also be written using the metapopulation reproduction ratio,

$$R(\hat{D}) = \frac{\sum \hat{F}(\xi, \hat{D}) p(\xi, \hat{D})}{\hat{D}}. \tag{8}$$

At equilibrium, $R(\hat{D}) = 1$ should be satisfied, since one disperser on average should produce exactly one dispersing descendant to maintain the metapopulation in equilibrium.

2.3.2. Metapopulation viability

We define a metapopulation to be viable if there exists a positive attractor for its dynamics. This condition necessarily holds if the extinction equilibrium $D = 0$ is unstable, i.e. when $R_0 > 1$, where

$$R_0 = \lim_{D \to 0} R(D). \tag{9}$$

At least for large values of D, $R(D)$ is a decreasing function. If $R(D)$ is decreasing for all D, then metapopulation viability can be uniquely determined from R_0. Specifically, if $R_0 > 1$, then there exists a unique positive equilibrium $\hat{D}$, but if $R_0 < 1$, then $R(D) < 1$ for all D, so no positive equilibria exist. However, if an Allee effect (Allee *et al.*, 1949) is present at the metapopulation level, it is possible that $R(D) = 1$ for a positive D even when $R_0 < 1$. For example, this situation arises when the catastrophe rate is a decreasing function of population size (see Fig. 3). For constant catastrophe rates, such a situation is unlikely in the present model since we have introduced no other individual-level mechanisms expected to create Allee effects. Our numerical results support this intuitive claim. Before seeking a detailed expression for R_0, we need to introduce some notation.

2.4. Invasion fitness in the metapopulation model

To analyse evolutionary dynamics of dispersal behaviour (emigration rate e) we apply the adaptive dynamics framework (Metz *et al.*, 1992, 1996; Geritz *et al.*, 1997, 1998). A core concept is the invasion fitness, defined by Metz *et al.* (1992) as the long-term exponential growth rate $r(e_{\mathrm{mut}}, E_{\mathrm{res}})$ of a rare mutant in the environment E_{res} set by a resident population. Mutations are so infrequent that the population dynamics always settles to an attractor defined by the residents before the next mutation occurs.

In metapopulation models, it is often convenient to operate on dispersing generations and use the metapopulation reproduction ratio R_{metapop} (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) as a proxy for invasion fitness. That is, when a mutant disperser immigrates from the dispersal pool onto a patch, it initiates a new local clan, which consists of the immigrant itself and all of its lineal descendants produced on that patch until the clan is destroyed by local patch extinction. Each surviving generation seeds the dispersal pool with new dispersers. Thus, $R_{\mathrm{metapop}}(e_{\mathrm{mut}}, E_{\mathrm{res}})$ is defined as the expected number of successful dispersers produced by an average local clan initiated by a mutant using strategy e_{mut} in an environment E_{res} set by the resident. A mutant population may invade the resident only when $r(e_{\mathrm{mut}}, E_{\mathrm{res}}) > 0$, or equivalently, $R_{\mathrm{metapop}}(e_{\mathrm{mut}}, E_{\mathrm{res}}) > 1$.

Metz and Gyllenberg (2001) and Gyllenberg and Metz (2001) explain how to calculate the metapopulation reproduction ratio in various continuous-time metapopulation models. Parvinen (2006) presents an analogous method for discrete-time metapopulation models. Here, we will explain how to extend these methods to our semi-discrete metapopulation model with continuous within-season dynamics.

2.4.1. Polymorphic model

To apply the theory above, we now extend our model to include multiple competing strategies. Our expanded model for the early summer season is the following:

$$\begin{cases} \dot{A}_i = -(\mu_A A_i + \gamma_{JA} J A_i), \\ \dot{J}_i = -(\mu_J J_i + (\gamma_{AJ} + \gamma_{JA}) J_i A + (\gamma_{JB} + \gamma_{BJ})\, J_i B + \beta J_i E + e_i J_i), \\ \dot{B}_i = \gamma_{JA} J_i A + \beta J_i E + \gamma_{JB} J_i B - \gamma_{JB} J B_i - \mu_B B_i, \\ \dot{F}_i = e_i J_i - \mu_J F_i, \end{cases} \tag{10}$$

where A_i, J_i, B_i, F_i stand for adults, unestablished juveniles, established juveniles and emigrants, respectively, having strategy or phenotype indexed by $i = 1, \dots, N$. The letters A, J, B and F without subscript denote the total number of pikas of each corresponding type; for example, for adults, $A = \sum_{i=1}^{N} A_i$.

As before, emigration stops at time τ_2, at which time immigration takes place. Thus, the equations for late summer do not include $\dot{F}_i$, and the equation for $\dot{J}_i$ in (10) becomes

$$\dot{J}_i = -(\mu_J J_i + (\gamma_{AJ} + \gamma_{JA}) J_i A + (\gamma_{JB} + \gamma_{BJ}) J_i B + \beta J_i E), \tag{11}$$

with initial value $J_i(\tau_2) = J_i(\tau_2 -) + \hat{D}_i$, where $\hat{D}_i$ is naturally the amount of juveniles with strategy e_i in the dispersal pool per patch. No other alterations are made to the monomorphic model.

2.4.2. Descendants of a mutant disperser

Assume that the resident population consisting of N phenotypes is at a known metapopulation-dynamical equilibrium. In that case, for all $i = 1, \ldots, N$ we know the dispersal pool sizes D_i, the patch age distribution $p(\xi)$, and the population sizes of adults $A_i(\xi, t)$, unestablished juveniles $J_i(\xi, t)$, and established juveniles $B_i(\xi, t)$ for all patch ages ξ as a function of the within-season time t. How do mutants perform in such an environment? What is their fitness proxy, the metapopulation reproduction ratio in the environment set by the resident population? This we will explain next in detail.

Consider the system (10) and (11) with $N+1$ phenotypes, but let us denote the index $N+1$ as 'mut' to emphasize that this is the mutant phenotype. Because the mutant population is rare, its effect on the resident population is insignificant. The mutant population dynamics is thus generated by (10) and (11), where the total population sizes A, J and B are obtained by summing over only the resident phenotypes. Because of the assumption above, these sizes are already known. As a result, the system of differential equations becomes linear with respect to the mutant population size.

To calculate the fitness proxy, we first need to calculate the probabilities $P_{D\to 1}(\xi)$ that a mutant in the dispersal pool will immigrate, become established, and survive until the next census, provided that the age of the patch into which it immigrates is ξ. It is obtained by solving (10) and (11) from time τ_2 to 1 with initial conditions $A_{\mathrm{mut}}(\xi, \tau_2) = J_{\mathrm{mut}}(\xi, \tau_2) = B_{\mathrm{mut}}(\xi, \tau_2) = 0$, and $\hat{D}_{\mathrm{mut}} > 0$:

$$P_{D\to 1}(\xi) = B_{\mathrm{mut}}(\xi, 1)/\hat{D}_{\mathrm{mut}}. \tag{12}$$

Without loss of generality we can assume that $\hat{D}_{\mathrm{mut}} = 1$.

Next we need to calculate the performance of adult mutants. Let $E_{A\to D}(\xi)$ denote the expected number of emigrating mutant juveniles per adult present at time $t = 0$ (at census) in a patch of age ξ. We thus use the initial conditions $A_{\mathrm{mut}}(\xi, 0) > 0$, and $J_{\mathrm{mut}}(\xi, 0) = B_{\mathrm{mut}}(\xi, 0) = 0$, take into account winter and reproduction, as explained in Section 2.2.1, and solve the system of differential equations (10) during the early summer $[\tau_1, \tau_2]$:

$$E_{A\to D}(\xi) = \pi F_{\mathrm{mut}}(\xi, \tau_2)/A_{\mathrm{mut}}(\xi, 0). \tag{13}$$

We continue to the late summer to obtain the expected number of adult mutants at the end of the season census ($t = 1$) per adult present at time $t = 0$ (at census) in a patch of age ξ. Because the mutants are globally rare, no mutant immigrants are expected to arrive into this patch, and thus we assume $J_{\mathrm{mut}}(\tau_2) = J_{\mathrm{mut}}(\tau_2 -)$. The total adults at the end of the season consist of the original adults themselves, if they manage to survive until time $t = 1$, and their philopatric offspring that become established and survive until time $t = 1$:

$$E_{A\to A}(\xi) = (A_{\mathrm{mut}}(\xi, 1) + B_{\mathrm{mut}}(\xi, 1))/A_{\mathrm{mut}}(\xi, 0). \tag{14}$$

Again, without loss of generality, we can assume $A_{\mathrm{mut}}(\xi, 0) = 1$.

Since immigrants choose patches at random, the patch into which an immigrant arrives has age ξ with probability $p(\xi)$. The patch goes extinct over winter with probability $\mu_c(A(\xi))$, so this mutant survives to the following year with probability $1 - \mu_c(A(\xi))$. This mutant will be the ancestor of a mutant lineage (also called a mutant clan) in this patch, currently of age $\xi + 1$. Let $E(\xi + 1)$ denote the cumulative number of emigrated mutant juveniles over all coming years in the lineage established by a single mutant ancestor. Using this notation we obtain the metapopulation reproduction ratio

$$R_{\mathrm{mut}} = \sum_{\xi=0}^{\infty} p(\xi) P_{D\to 1}(\xi)(1-\mu_c(A(\xi)))E(\xi+1), \tag{15}$$

which is the expected number of all future dispersing descendants of a mutant immigrant in a resident population at equilibrium.

We still need to be able to calculate $E(\xi)$, the cumulative number of emigrated mutant juveniles over all coming years in the lineage established by a single mutant ancestor in a patch of age ξ. A part of this quantity is the disperser production during the current year $E_{A\to D}(\xi)$. Next, the expected number of adults present in this patch in the next year is obtained by multiplying $E_{A\to A}(\xi)$ with the probability that a catastrophe does not occur during winter, $1-\mu_c(A(\xi))$. In this case, the age of this patch next year is $\xi+1$, and the cumulative number of emigrated mutant juveniles in the lineages each of the adults will initiate is equal to $E(\xi+1)$. Analogous to Parvinen (2006), we thus obtain the recursive equation,

$$E(\xi) = E_{A\to D}(\xi) + E_{A\to A}(\xi)(1-\mu_c(A(\xi)))E(\xi+1). \tag{16}$$

To complete the calculation we only need a starting point of the recursion. Unfortunately, we do not know $E(0)$. If, however, we know $E(\hat{\xi})$ for some large $\hat{\xi}$, we can calculate $E(\xi)$ for all $\xi = 0, 1, \ldots, \hat{\xi}-1$ using the recursion (16). For large ξ, the local population approaches an attractor, which under the present assumptions is an equilibrium. That is, there exists an age L for which $|A(0, L) - A(0, \xi)|$ is sufficiently small for every $\xi > L$. In most cases, we have used $L = 100$. In case this is observed not to be sufficiently large (from $R_{\mathrm{mut}} \neq 1$ for $e_{\mathrm{mut}} = e_{\mathrm{res}}$), we have used $L = 400$. The quantities are continuous functions of the initial resident population sizes $A(0, \xi)$. Therefore, $E_{A\to D}(\xi) \approx E_{A\to D}(L)$ and $E_{A\to A}(\xi) \approx E_{A\to A}(L)$ for $\xi > L$. Assuming $E(\xi+1) = E(\xi)$, equation (16) can be rewritten as

$$E(\xi) = \frac{E_{A\to D}(L)}{1-(1-\mu_c(A(L)))E_{A\to A}(L)}, \qquad \text{for } \xi > L. \tag{17}$$

This gives us our initial $E(\hat{\xi})$. After calculating the values of $E(\xi)$ for all $\xi = 0, 1, \ldots, \hat{\xi}-1$ from (16), we obtain the proxy for invasion fitness from (15).

2.4.3. Population viability

As mentioned earlier (equation 9), the metapopulation extinction equilibrium is unstable if $R_0 > 1$, where $R_0 = \lim_{D\to 0} R(D)$ is obtained as a limit of the resident metapopulation reproduction ratio (8) for an infinitesimally small resident metapopulation. When presenting the method to calculate the fitness of a mutant, we have also introduced the notation needed in the calculation of R_0. This quantity can also be seen as the invasion fitness proxy of a mutant in a virgin environment.

We can show that the limit $R_0 = \lim_{D\to 0} R(D)$ of the resident metapopulation reproduction ratio (8) is equal to the mutant fitness proxy (15) in the virgin environment, $R_{\mathrm{mut}}(s_{\mathrm{res}}, E_0)$, and can be written as

$$R_0 = \begin{cases} \dfrac{P_{D\to 1}E_{A\to D}}{(1-\mu_c(0))^{-1} - E_{A\to A}}, & \text{if} \quad E_{A\to A} < \dfrac{1}{1-\mu_c(0)}, \\ \infty, & \text{otherwise} \end{cases} \tag{18}$$

where the quantities $P_{D\to 1}$, $E_{A\to D}$ and $E_{A\to A}$ are obtained from (12), (13) and (14), respectively, without a resident population ($A = J = B = 0$). The proof can be found in the Appendix. The expected number of dispersers emigrating at the ξth year after the foundation of the clan is proportional to $A(\xi)(1 - \mu_c(0))^{\xi}$ (using the notation in the Appendix). When $(1 - \mu_c(0))E_{A\to A} > 1$, this amount will increase with ξ, thus causing the patch life-time production of dispersers to be infinite. Note that this does not mean infinitely fast real-time population growth. See also the equation (15) of Gyllenberg *et al.* (2002).

3. RESULTS

We begin our investigation by assessing how average local population size depends on various model parameters. Then we evaluate the qualitative and quantitative effects of changes in these parameters on evolution of dispersal (emigration rate *e*). Both ecological and evolutionary analyses are done for both constant and population-size-dependent patch extinction rates.

3.1. Population size

Variations in mean patch population sizes at equilibrium at the time of the census, viz. $\bar{A} = \sum_{\xi=0}^{\infty} A(1, \xi)p(\xi)$, are shown in Fig. 3a–d for the case in which catastrophic extinction rate does not depend on patch population size. In this case, mean patch population size, or equivalently total population size, tends to be a unimodal function of emigration rate, suggesting a typically finite ‘optimal’ dispersal rate *vis-à-vis* population size. Excessively high dispersal rates can drive the metapopulation to extinction (e.g. Fig. 3b–d), in essence because too many organisms are risking a dangerous dispersal episode. Therefore, population size and the domain of metapopulation viability critically depends on changes in disperser survival probability (π; Fig. 3c). On the other hand, if dispersal rates become too small, then the metapopulation goes extinct as colonization rate fails to match patch extinction rate. Therefore, mean local patch occupancy, and therefore metapopulation size, reaches its maximum for intermediate emigration rates (Fig. 3a–d).

Interestingly, the rate at which unestablished juveniles challenge adults, $\hat{\gamma}_{JA}$, has a significant negative influence on population size (Fig. 3a). As juveniles challenge adults, adult mortality increases, but each adult lost is replaced by the winning juvenile. Thus, the adult mortality is compensated. However, with lower $\hat{\gamma}_{JA}$, juveniles would find an empty site instead of challenging adults. This is better not only for the adults but also for those juveniles who would be losers in a challenge. On the other hand, juvenile–juvenile challenge rate ($\hat{\gamma}_{JB}$) and the probability of successful usurpation (p_1 and p_2) have much less drastic effects (results not shown). In particular, events where juveniles challenge established juveniles affect equation (1) only through the factor $\gamma_{JB} + \gamma_{BJ} = \hat{\gamma}_{JB}(p_2 + (1 - p_2)) = \hat{\gamma}_{JB}$. Thus the parameter p_2 has no effect at all on the monomorphic population dynamics, because at the population level it does not matter which juvenile wins. Note, however, that p_2 is present in the analogous polymorphic equations (10).

The parameter β describes how efficiently juveniles find and settle empty territories. Not surprisingly, this parameter strongly affects equilibrium population size and viability (Fig. 3b). If β is too low (below approximately 0.5 when all the other parameters are fixed at their default values), the metapopulation is not viable. For larger values, the metapopulation becomes viable, and $\bar{A}$ is an increasing function of β. The mean size $\bar{A}$

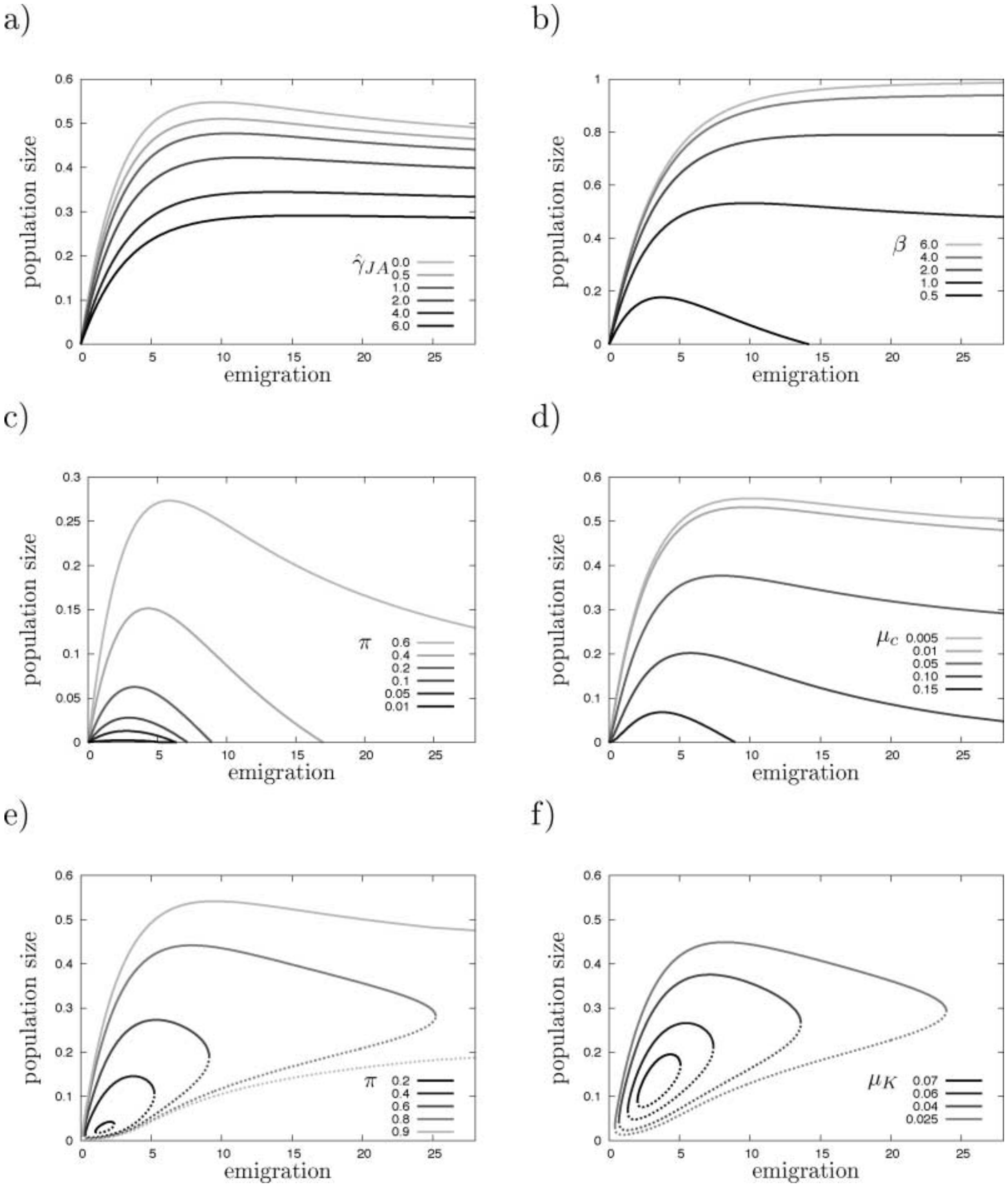

Fig. 3. Average population size at census time with respect to emigration rate for several values of (a) attack rate $\hat{\gamma}_{JA}$, (b) colonization rate β, (c) dispersal survival π and (d) catastrophe rate μ_c, when the catastrophe rate is assumed not to depend on the local population size. Similarly, average population size for several values of (e) dispersal survival π and (f) catastrophe rate in full patches μ_K, when the catastrophe rate is assumed to depend on the local population size according to (7). Other parameters have their default value (Table 2). Curves for different parameter values are drawn with different grey scale, as described in the corner of each panel. Attractors are drawn with a solid curve, and repellors with a dotted curve.

approaches an asymptotic limit as β gets large, since $\beta \to \infty$ means that all empty sites will be immediately occupied.

As expected, mean local population size and metapopulation viability depend heavily on patch extinction rates (μ_c). This result follows from basic metapopulation theory – metapopulations are viable only if colonization rates exceed patch extinction rates (Levins, 1969).

In contrast to the case with a constant catastrophe rate (Fig. 3a–d), dramatically different results are seen (Fig. 3e, f) when catastrophe rate depends on local population density according to (7). In the latter case, the metapopulation becomes inviable through a fold bifurcation when emigration rates are either too low or too high, and the extinction equilibrium is then globally asymptotically stable. For intermediate emigration rates, an additional pair of positive metapopulation-dynamical equilibria exist: a repellor and an attractor. The metapopulation extinction equilibrium remains in this case locally stable. In the example in Fig. 3e, f, the catastrophe rate in sparsely populated patches is rather high, but is much lower in densely populated patches. Such population-size dependent catastrophe rates generate an Allee effect. For pikas, we find this type of catastrophe rate more realistic than the constant one because in the Bodie metapopulation, small patches are significantly more likely to go extinct than larger ones (Smith and Gilpin, 1997). Again, dispersal survival, π, has a positive effect on the population size (Fig. 3e); both the equilibrium local population densities and the region of viable emigration strategies are increasing functions of π. If π is too low, the metapopulation is not viable for any emigration rate. A similar phenomenon is observed in Fig. 3f. In this case, population density at equilibrium and the zone of viability are decreasing functions of the catastrophe rate in full patches, μ_K.

3.2. Evolution of dispersal

In this section, we investigate the adaptive dynamics of dispersal in the pika metapopulation model. We also use the resulting pairwise invasibility plots (PIP) (Matsuda, 1985; Van Tienderen and De Jong, 1986) and bifurcation diagrams to initiate an analysis of various putative effects of global climate change on selection for dispersal in pika metapopulations and its subsequent impact on metapopulation dynamics.

In a PIP (e.g. Fig. 4), the horizontal and vertical axis represent the resident's and mutant's strategies, respectively. In regions shaded dark grey, mutant strategies can invade, but in regions shaded light grey, they cannot. Evolutionarily singular strategies (Maynard Smith, 1976, 1982; Maynard Smith and Price, 1973; Eshel, 1983; Christiansen, 1991; Geritz *et al.*, 1997, 1998) are points for which the fitness gradient is zero. On the PIP, these points are identified by the intersection of two zero-contours: one the identity line and the other not. Regions for which a resident population is not viable are shaded grey and demarcated with vertical lines (see, for example, Fig. 5).

In the case of a constant catastrophe rate, there typically exists a unique singular strategy, which is uninvadable (ESS) and evolutionarily attracting from all viable initial strategies. A pairwise invasibility plot for the default parameters is shown in Fig. 4, in which case the evolutionary endpoint is at $e^* \approx 0.502$.

This situation becomes more realistic, but also more complicated, when we consider catastrophe rates that depend on local population size. In such cases, it is possible that both the lower and upper boundaries of viability are evolutionarily repelling, and there exists a unique attracting ESS (Fig. 5a). However, one can observe a characteristic series of evolutionary bifurcations with variations in parameters. For example, as disperser survival π

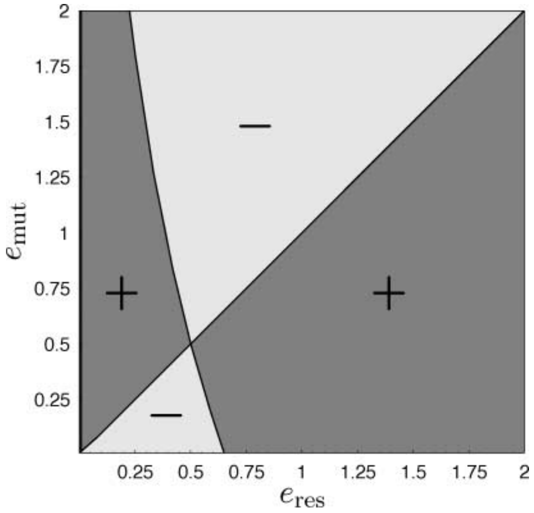

Fig. 4. Pairwise invasibility plot (PIP) with constant catastrophe rate, default parameter values.

decreases, first the lower boundary of viability becomes evolutionarily attracting, and a repelling singular strategy appears (Fig. 5b). The larger singular strategy remains an attractor. If the initial strategy is exactly the repelling point, no mutant can invade. However, if the initial strategy is slightly to either side of the repellor, traits further away may invade, resulting in a repelling sequence of trait substitutions. Such a repelling singularity is called a Garden of Eden (Hofbauer and Sigmund, 1990). As π continues to decrease, the attracting and the repelling singular strategies collide and disappear (Fig. 5c) at approximately $\pi = 0.70$. For $\pi < 0.70$ (Fig. 5d), the metapopulation is doomed to extinction through evolutionary suicide (Ferrière, 2000; Gyllenberg and Parvinen, 2001; Gyllenberg *et al.*, 2002; Parvinen, 2005) regardless of initial condition, because any resident strategy can be invaded and replaced by a mutant with a smaller dispersal rate. Therefore, the trait substitution sequence will eventually lead to the lower boundary of viability. At this point it is still true that a mutant with a lower emigration rate can invade and eventually dominate. But this mutant is not viable as a resident, so this invasion will lead the whole metapopulation to extinction.

Next, we continue in this vein to explore how disperser survival, catastrophes, fecundity or overwinter mortality affect the location of boundaries of viability and singular strategies.

3.2.1. Dispersal survival π

The most obvious potential effect of global climate change on dispersal evolution is its potential to alter direct costs of dispersal, as Smith (1974b, 1980) has shown that pika vagility is lower at Bodie compared with higher, colder areas in the nearby Sierra Nevada. When catastrophe rates are fixed, all investigated viable metapopulations have a unique, attracting, evolutionarily stable singular strategy. As expected, the riskier it is to disperse, the less individuals will do so at evolutionary equilibrium. Not surprisingly, then, the singular strategy is an increasing function of π (Fig. 6a).

When catastrophe rates are size-dependent, we see a bifurcation point at $\pi \approx 0.2$ (Fig. 6b; here the results in Fig. 5 are reassembled in a bifurcation diagram). To the left, the

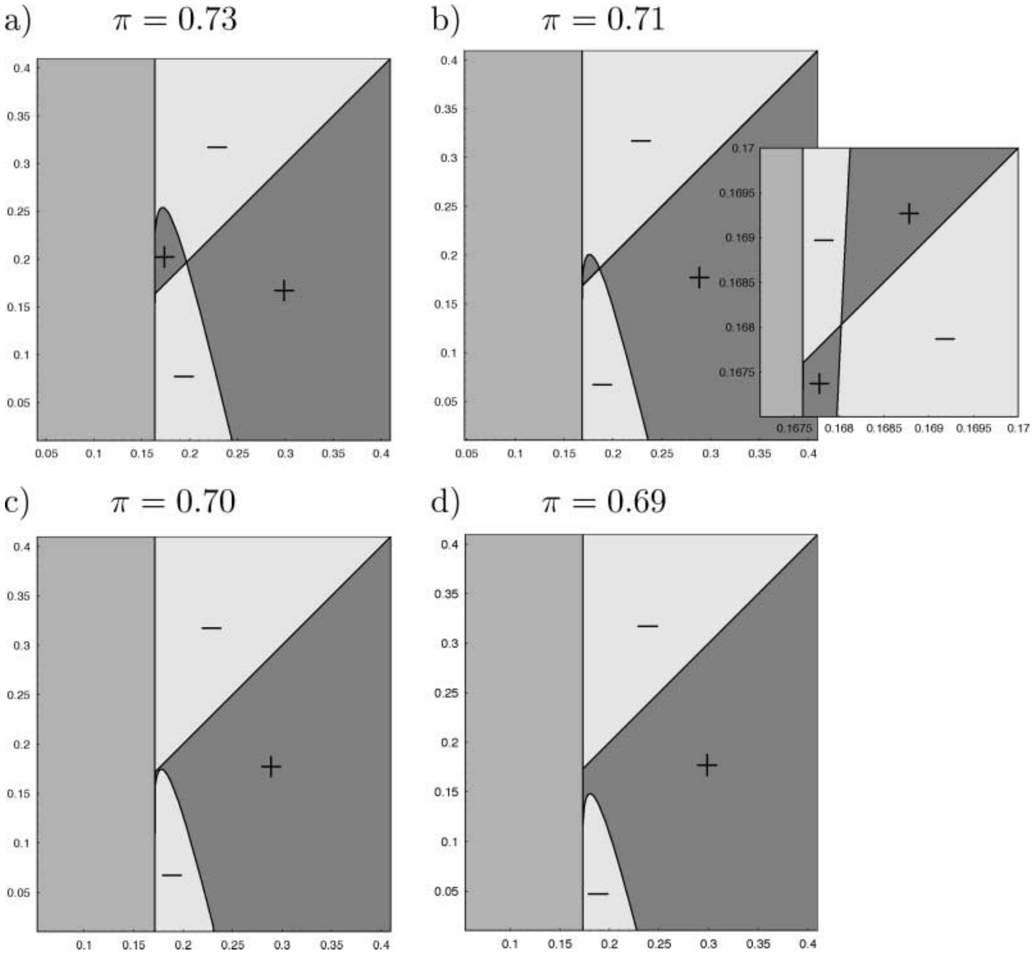

Fig. 5. Pairwise invasibility plots with different values of π, when the catastrophe rate is assumed to depend on the local population size according to (7). The lower boundary of viability is shown as a vertical line. Observe the repellor in the inset of panel b ($\pi = 0.71$).

population is inviable for any strategy. To the right, as π increases, upper and lower boundaries of viability appear and separate from each other. Just to the right of this population bifurcation, there is no attracting evolutionary singular strategy in the viability region, and the lower viability boundary is an evolutionary attractor. Hence, the metapopulation is guaranteed to go extinct due to evolutionary suicide. Biologically, the costs of dispersal are so high that natural selection depresses the dispersal rate beyond what is required for population survival. Continuing to the right there is an evolutionary bifurcation, where attracting and repelling (Garden of Eden) singular strategies arise (Fig. 6b and c). This situation is limited, however. As π increases, the repelling Garden of Eden singularity approaches and finally collides with the lower viability limit. Beyond this second evolutionary bifurcation (to the right), both viability boundaries are repelling, and evolutionary trajectories approach the singular strategy.

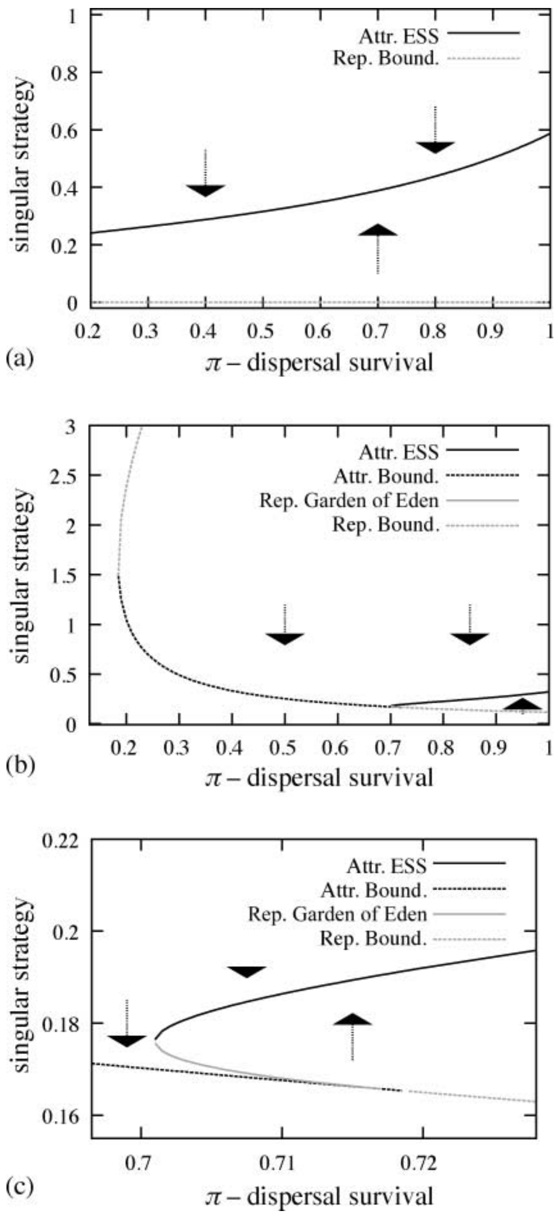

Fig. 6. Singular dispersal strategies (attracting ESS with black solid line, repelling Garden of Eden with grey solid line) and boundaries of viability (attracting boundary with black dotted line, repelling boundary with grey dotted line) with respect to dispersal survival π. In panel (a) the catastrophe rate is population-size independent, whereas in the two other panels the catastrophe rate depends on the local population size according to equation (7). Inset of the bifurcation diagram in panel (b) is shown in (c). An attracting ESS and a repelling singularity (Garden of Eden) exist for π large enough, but when π decreases, these two singularities collide and disappear. The same evolutionary bifurcation is also illustrated in Fig. 5.

3.2.2. Catastrophe rate

Global climate change may also alter patch catastrophe rate, since such catastrophes are most likely due to excessively early or late snowmelt and other effects on precipitation (Smith, 1980, 1987). Catastrophes result in empty or sparsely populated patches with little competition for territories. Therefore, increasing the catastrophe rate could be expected to increase selection for dispersal. Indeed, this expectation is largely correct, but when catastrophe rates are population size-independent, the singular dispersal strategy becomes a unimodal function of catastrophe rate, increasing with the catastrophe rate only when these rates are small (Fig. 7a). Such non-monotonic effects of catastrophes on singular strategies have already been found in several models (Ronce *et al.*, 2000; Gyllenberg *et al.*, 2002; Parvinen *et al.*, 2003; Parvinen, 2006). A heuristic explanation (Parvinen *et al.*, 2003) is that when catastrophes are frequent, most individuals already live in sparsely populated patches; thus, the benefits of dispersal will eventually decrease as catastrophe rate increases, but the costs are unaffected. On the other

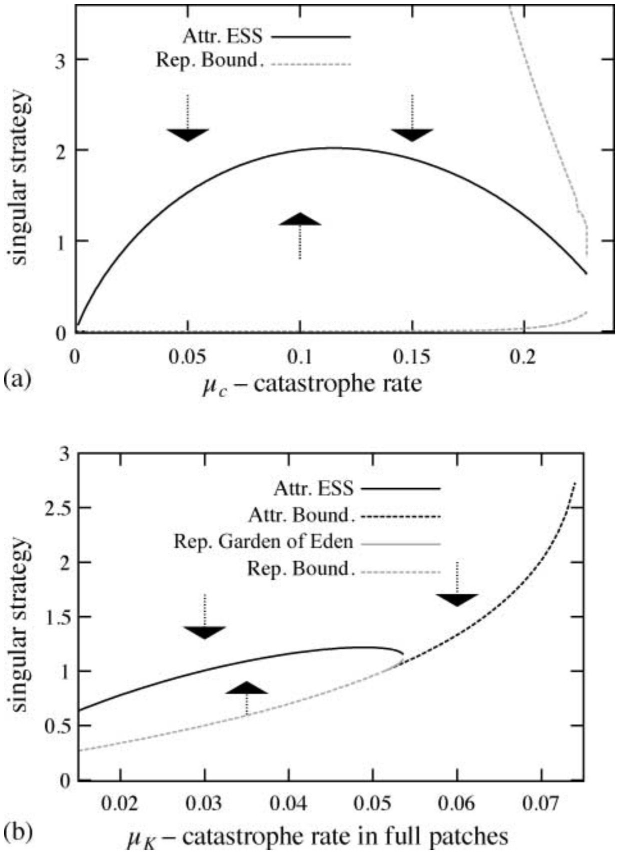

Fig. 7. Singular dispersal strategies (attracting ESS with black solid line, repelling Garden of Eden with grey solid line) and boundaries of viability (attracting boundary with black dotted line, repelling boundary with grey dotted line) with respect to (a) constant catastrophe rate μ_c and (b) catastrophe rate in fully occupied patches μ_K in the case of density-dependent catastrophe rate (7). A similar evolutionary bifurcation as illustrated in Fig. 6b and 6c occurs here in panel (b), when μ_K is approximately 0.055.

hand, in metapopulation models without catastrophes, dispersal is not expected to arise if no other mechanism selecting for dispersal – like environmental or demographic stochasticity, or non-equilibrium local population dynamics providing variability in the local environments in patches – is present. When all patches are equal, there is no 'better' place for dispersers to go.

In the case of population-size dependent catastrophes (Fig. 7b), we alter the catastrophe rate in full patches, μ_K. Unsurprisingly, the metapopulation is inviable if the catastrophe rate is too high (greater than about 0.075). As catastrophe rates decline, the metapopulation is initially viable, but natural selection will eventually cause evolutionary suicide as dispersal rate is pushed into the inviable region. As the value of μ_K decreases, several evolutionary bifurcations occur similar to those seen in Fig. 6b with respect to π. In particular, two singular strategies arise at the bifurcation point ($\mu_K \approx 0.053$): one evolutionary attractor and one Garden of Eden. As the catastrophe rate declines, the Garden of Eden very quickly collides with the lower viability boundary, causing it to switch (as before) from (locally) stable to unstable. The interesting thing here from the biological perspective is that the catastrophe rate has a very small impact on the magnitude of dispersal. Although catastrophes tend to increase the benefits of dispersal by providing competition-free outlets for dispersers, these sparsely populated patches are also most vulnerable to catastrophes. So the effect of increasing catastrophes on costs of dispersal can outweigh the benefits if the catastrophe rate depends on the local population size.

3.2.3. Fecundity and overwinter mortality

Since global climate change also alters precipitation, it may also affect pika fecundity indirectly via its effects on food resources. Such changes may affect fecundity by changing the nutritional state of female pikas during critical periods of gestation and lactation, and may also alter the nutritional quality of hay, thereby impacting the animals' ability to withstand the physiological rigours of winter. Thus, we explore here the effect of changes in fecundity and overwinter mortality on the evolution of dispersal and metapopulation viability.

Unsurprisingly, population viability requires a sufficiently high fecundity (Fig. 8a). If catastrophe rate is constant, then the singular strategy appears to be an increasing function of fecundity (not illustrated). As usual, the situation becomes more complicated in the more realistic case in which catastrophe rates are size-dependent. The bifurcation diagram with fecundity as the bifurcation parameter is very similar to the case in which disperser survival is the bifurcation parameter (Fig. 6b) – first a viability bifurcation arises, then an evolutionary bifurcation occurs resulting in Garden of Eden and attracting singular strategies, followed by collision of the Garden of Eden and attracting viability boundary, switching that boundary to a repellor, all as fecundity increases. Similarly, the bifurcation diagram for variation in overwinter mortality (Fig. 8b) shows a similar pattern of bifurcations.

4. DISCUSSION

We are led to modelling pika populations by the open debate over the threat global climate change poses to the American pika, especially in the Great Basin and Sierra Nevada. The mountainous regions where pikas live are expected to be among those that experience the greatest impact from global climate change, and thus pikas could act as a 'canary'

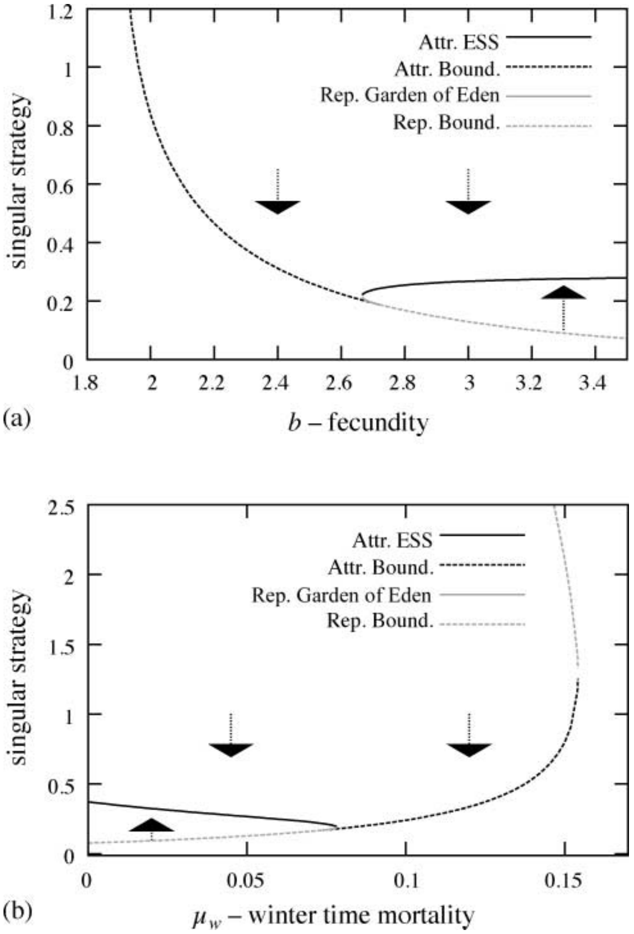

Fig. 8. Singular dispersal strategies and boundaries of viability with respect to (a) fecundity and (b) overwinter mortality in the case of density-dependent catastrophe rate. (Line style description as for Figs. 6 and 7.) A similar evolutionary bifurcation as illustrated in Fig. 6b and 6c occurs here in (a) when b is approximately 2.7 and in (b) when μ_w is approximately 0.075.

indicator for the effects of climate change. On the other hand, these effects are largely unpredictable, and as the contradictory evidence noted in the Introduction warns, the situation is liable to be very complex. Certainly, it is not clear at the moment what sort of change and what magnitude of change global climate change will have on the relevant biology of pikas. Climate change may increase or decrease fecundity; it may increase or decrease patch population extinction rates; it may increase or decrease pika mortality rates; it may alter both the costs and benefits of dispersal. It is clear we need more basic data. From the population dynamics perspective, we need to know how global climate change is affecting fecundity, mortality and dispersal, both directly and indirectly. Lacking such basic data, one job of the theoretician is to tease apart the complexity with models, and use these to predict which types of changes to these basic parameters are likely to have the greatest impact, and also to explore and expose subtle interactions that otherwise would go unheeded.

To this end, we have constructed a novel semi-discrete metapopulation model to study the effects of changes in fecundity and mortality on the evolution of dispersal in a context suitable for application to a pika metapopulation. In particular, the model is formulated in semi-discrete time, i.e. mortality and dispersal are continuous processes, although they may change discontinuously at discrete time points, and births occur at discrete time points. Our model is deterministic by its nature, capturing the basic life cycle features of the American pika. Our model parameters are not retrieved directly from field data. However, they are generally at least of the correct order of magnitude or better based on existing natural history information available in the literature (Barash, 1973; Smith, 1974a, 1974b, 1978, 1980; Smith and Ivins, 1983; Smith and Weston, 1990). Nevertheless, we vary many within their realistic range to explore the influence of changing parameters on ecological and evolutionary dynamics.

In particular, these variations represent potential effects of global climate change, so we focus our variations specifically on catastrophe, mortality and fecundity rates. We chose these because of their central importance to metapopulation dynamics. However, we do not – indeed could not – speculate about the precise effect of global climate change on these parameters. Instead, we take a general view and explore, using an adaptive dynamics framework, how variation in certain key parameters would affect the evolution of dispersal in a general pika metapopulation. Even though evolutionary dynamics might be slow compared with environmental changes, we believe that by this approach we can generate new insights relevant to sustainability and management of pikas and other vertebrate metapopulations.

Interestingly from the biological perspective, results from the case in which extinction risk declines with population size (Figs. 6b, 7b and also 8) suggest that a metapopulation dynamical analysis alone could be misleading in the face of global climate change. Consider, for example, Fig. 8a. If the birth rate lies between 1.91 and about 2.67, sufficient dispersal repopulates sparsely inhabited patches, making them relatively densely populated. Therefore, dispersal not only increases colonization rate, but it also decreases patch extinction risk, both of which help to maintain metapopulation viability by the classical Levins mechanism. However, for an individual pika living in such a population, the individual costs of dispersal outweigh the benefits. So here we see a classic conflict between the interests of groups (patches) and individuals. As is typical in such conflicts, individual interests trump the interests of the group, because natural selection acts on the level of individuals (Williams, 1966). Since selection favours individuals with ever-lower dispersal propensities, colonization rates eventually drop below patch extinction rates, causing extinction of the entire metapopulation via evolutionary suicide.

Now, consider a pika metapopulation with a birth rate around 2.75 behaving according to the attracting singular dispersal propensity of about 0.25. If global climate change or some other force were to rapidly drop pika fecundity to, say, 2.65 for example, again a metapopulation dynamical analysis will tend to indicate that the pika population is viable, since the current dispersal propensity is sufficient to maintain colonization rates above extinction rates. However, taking the evolutionary dynamics of dispersal into account, the model suggests that the metapopulation is, as above, doomed to commit evolutionary suicide. Note that changes in fecundity are not the only mechanisms capable of causing potentially unanticipated evolutionary suicide. Similar scenarios could arise through changes in disperser survival (Fig. 6b), catastrophe rate in full patches (Fig. 7b) and overwinter mortality (Fig. 8b), in addition to the picture painted above. Indeed, this type of scenario appears to be a common feature of the model in which local population extinction rates depend on local population size.

In addition, the existence of the Garden of Eden suggests that even if the population is viable and even when there exists an attracting evolutionary strategy in the viable region, if the change caused by global climate change is large enough the system could perhaps end up on the wrong side of the evolutionary repellor, and the population would again be destined for extinction via evolutionary suicide (Ferrière, 2000; Gyllenberg and Parvinen, 2001; Gyllenberg *et al.*, 2002; Webb, 2003; Parvinen, 2005). The mechanism behind this phenomenon is similar to the one explored by Gyllenberg *et al.* (2002). Indeed, it is interesting that the phenomenon of Darwinian extinction is an option to be considered not only in abstract models, but also in contexts tailored to real-world populations as in this study.

If agencies responsible for monitoring and evaluating the health of a metapopulation in evolutionary scenarios such as these measure only the current ecological parameters – current dispersal rates in particular – and not the entire evolutionary picture, they may miss the threat of evolutionary suicide if current dispersal rates support metapopulation viability. Given our lack of knowledge of the effects of global climate change on pikas, we do not suggest, however, that this line of argument applies to the Bodie metapopulation; rather, we simply sound a note of caution – here is an example in which evolutionary dynamics matter in the context of sustainability. Nevertheless, in the context of the Bodie pikas, as well as other populations in the Great Basin and Sierra Nevada, dispersal evolution must be considered when evaluating the viability of pika metapopulations, since exclusive reliance on metapopulation dynamical analysis will tend to overestimate the region of viability if global climate change has a major detrimental impact on these parameters. We see this as one of the most important predictions of this model so far.

Note that, despite our focus on pika metapopulations, the model as formulated can apply to many vertebrate species. In particular, the model can be modified to describe any territorial species with a discrete breeding season where natal dispersal occurs in a fragmented landscape. An important extension of the model would include a more general spatial structure. Although pikas at Bodie live in a (nearly) classical metapopulation, it appears that most Great Basin pikas live in insular Pleistocene remnant populations that rarely fit the criteria of a metapopulation in an obvious way. In particular, these remnants are unlikely to be connected by any significant dispersal. Instead, each population consists of a spatially complex, irregular pattern of patches of various sizes and shapes, often partially or completely connected to other patches by ‘isthmuses’. In contrast, the classic Sierra Nevada habitat consists of an enormous array of continuous or semi-continuous patches, with some discrete ‘islands’ near large ‘mainlands’, with irregular borders and variable aspect, microclimate and quality. Future efforts will adapt the model constructed here to describe these other, more typical spatial structures.

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APPENDIX: PROOF CONCERNING R_0

Stability of the extinction equilibrium

In the main text we presented the result that the fitness of a mutant in the virgin environment $R_{\text{metapop}}(s_{\text{mut}}, E_0)$ is equal to $R_0 := \lim_{D\to 0} R(D)$, and gave the equation (18) for its calculation. We will next prove this result, starting from the expression $R_{\text{metapop}}(s_{\text{mut}}, E_0)$.

Mutant's fitness in virgin environment When there is no resident present, our ODE system (10) for a rare mutant alone reduces to

$$\begin{cases} \dot{A}_{\text{mut}} = -\mu_A A_{\text{mut}} \\ \dot{J}_{\text{mut}} = -\mu_J J_{\text{mut}} - \beta J_{\text{mut}} K - e_{\text{mut}} J_{\text{mut}} \\ \dot{B}_{\text{mut}} = -\mu_B B_{\text{mut}} + \beta J_{\text{mut}} K \end{cases} \tag{19}$$

together with $\dot{F}_{\text{mut}} = e_{\text{mut}} J_{\text{mut}} - \mu_J F_{\text{mut}}$ for the early summer season, and

$$\dot{J}_{\text{mut}} = -\mu_J J_{\text{mut}} - \beta J_{\text{mut}} K \tag{20}$$

with the initial value $J_{\text{mut}}(\tau_2) = J_{\text{mut}}(\tau_2 -) + D$ for the later summer season. Since there are no residents and the mutant is rare, all patches are empty and equal (corresponding to $p(0) = 1$) when a mutant immigrant enters a patch. Hence, equation (15) becomes

$$R_{\text{mut}} = \sum_{\xi=0}^{\infty} p(\xi) P_{D\to 1}(\xi)\,(1-\mu_c) E(\xi+1) = P_{D\to 1}(1-\mu_c(0))E, \tag{21}$$

because the quantities $P_{D\to 1}(\xi)$ and $E(\xi+1)$ no longer depend on ξ. Assuming $E(\xi+1) = E(\xi)$ in equation (16), we get equation (17). Using that we obtain

$$R^0_{\mathrm{mut}} = \begin{cases} \dfrac{P_{D\to 1}E_{A\to D}}{\dfrac{1}{1-\mu_c(0)} - E_{A\to A}}, & \text{if } E_{A\to A} < \dfrac{1}{1-\mu_c(0)} \\ \infty, & \text{otherwise} \end{cases} \tag{22}$$

where all necessary quantities can be calculated analytically as follows:

Calculation of $P_{D\to 1}$ Let us first study what is the probability for a mutant in the disperser pool at time τ_2 to become established in a territory. For this reason, we look at the differential equations (19) and (20) of the reduced model for the later season with initial conditions $A(\tau_2) = 0$, $B(\tau_2) = 0$ and $J(\tau_2) = \hat{D} = 1$. Now the solution of the system is $A(t) = 0$ together with

$$\begin{aligned} J(t) &= e^{-(\mu_J + \beta K)(t-\tau_2)} \\ B(t) &= \frac{\beta K}{\mu_B - \mu_J - \beta K}\left(e^{-(\mu_J+\beta K)(t-\tau_2)} - e^{-\mu_B(t-\tau_2)}\right) \end{aligned} \tag{23}$$

from which we obtain

$$P_{D\to 1} = B(1). \tag{24}$$

Calculation of $E_{A\to D}$ Let us next look at the performance of adults present in a patch at the previous census. We solve the system of differential equations (19) and (20) for the early season with initial conditions $A(\tau_1) = 1 - \mu_w$, $J(\tau_1) = b(1-\mu_w)$ and $B(\tau_1) = 0$ and obtain

$$A(t) = (1-\mu_w)e^{-\mu_A(t-\tau_1)} \tag{25}$$

and

$$\begin{aligned} B_{\mathrm{early}}(t) &= \frac{\beta K b(1-\mu_w)}{\mu_B - \mu_J - \beta K - e_{\mathrm{mut}}}\left(e^{-(\mu_J+\beta K+e_{\mathrm{mut}})(t-\tau_1)} - e^{-\mu_B(t-\tau_1)}\right) \\ J_{\mathrm{early}}(t) &= b(1-\mu_w)e^{-(\mu_J+\beta K+e_{\mathrm{mut}})(t-\tau_1)} \\ F_{\mathrm{early}}(t) &= \frac{e_{\mathrm{mut}}b(1-\mu_w)}{e_{\mathrm{mut}} + \beta K}\left(e^{-\mu_J(t-\tau_1)} - e^{-(\mu_J+\beta K+e_{\mathrm{mut}})(t-\tau_1)}\right) \end{aligned} \tag{26}$$

from which we obtain the amount of dispersed offspring of the adult

$$E_{A\to D} = \pi F_{\mathrm{early}}(\tau_2). \tag{27}$$

Calculation of $E_{A\to A}$ Now we investigate what happens to the adult and its offspring remaining in their natal patch. We thus continue solving the system of differential equations (19) and (20), but now for the later season. Let initial values $A(\tau_2)$, $J(\tau_2)$ and $B(\tau_2)$ for the later season be those at the end of the early season. Since events affecting adults remain the same in the later season, the solution (25) is valid also during the later season. The solutions for J and B are

$$\begin{aligned} J_{\mathrm{later}}(t) &= J_{\mathrm{early}}(\tau_2)e^{-(\mu_J+\beta K)(t-\tau_2)} \\ B_{\mathrm{later}}(t) &= \frac{\beta K J_{\mathrm{early}}(\tau_2)}{\mu_B - \mu_J - \beta K}\left(e^{-(\mu_J+\beta K)(t-\tau_2)} - e^{-\mu_B(t-\tau_2)}\right) + B_{\mathrm{early}}(\tau_2)e^{-\mu_B(t-\tau_2)} \end{aligned} \tag{28}$$

from which, together with (25), we obtain the expected amount of adults in the end of the season

$$E_{A\to A} = A(1) + B_{\text{later}}(1), \tag{29}$$

which consists of the probability that the initial adult survives until the end of the season together with the amount of its offspring remaining in the natal patch which manage to occupy a territory.

The limit of the resident's fitness $R_0 := \lim_{D\to 0} R(D)$ We will next study what happens to the resident fitness $R(D)$ from equation (8) when the dispersal pool size D tends to zero. Assume that D is very small. Therefore, the quantities $P_{D\to 1}$, $E_{A\to D}$ and $E_{A\to A}$ do not depend on ξ, and can be calculated analytically as above. At the time of census, in a patch, there are juveniles which have survived after immigration and established themselves and adults which survived from the previous census. Thus, the amount of adults $A(\xi)$ in a patch of age ξ satisfies the recursion

$$A(\xi+1) = D\cdot P_{D\to 1} + A(\xi)\cdot E_{A\to A} \tag{30}$$

with the initial condition $A(0) = D\cdot P_{D\to 1}$. For convenience, let $C(\xi)$ denote the amount of adults in patches of age ξ at the beginning of the season, thus $C(0) = 0$ and $C(\xi) = A(\xi - 1)$. The solution of the recursion (30) can be written as a geometric sum (see also Table A1):

$$A(\xi) = D\cdot P_{D\to 1}\cdot \sum_{i=0}^{\xi} E^{i}_{A\to A} = D\cdot P_{D\to 1}\cdot \frac{1 - E^{\xi+1}_{A\to A}}{1 - E_{A\to A}}. \tag{31}$$

The number of juveniles, which arrive in the dispersal pool from the patch of age ξ, is

$$\hat{F}(\xi, D) = C(\xi)E_{A\to D} = A(\xi - 1)\cdot E_{A\to D}. \tag{32}$$

The reproduction ratio (8) is now

$$\begin{aligned}
R_0 &= \frac{1}{D}\Sigma_{\xi=1}^{\infty}\,\hat{F}(\xi, D)\mu(1-\mu)^{\xi}\\
&= \frac{E_{A\to D}P_{D\to 1}\mu}{1 - E_{A\to A}}\Sigma_{\xi=1}^{\infty}\Big((1 - E^{\xi}_{A\to A})(1-\mu)^{\xi}\Big)\\
&= \frac{E_{A\to D}P_{D\to 1}\mu}{1 - E_{A\to A}}\Sigma_{\xi=1}^{\infty}\Big((1-\mu)^{\xi} - (E_{A\to A}(1-\mu))^{\xi}\Big)\\
&= \frac{E_{A\to D}P_{D\to 1}\mu}{1 - E_{A\to A}}\left(\frac{1-\mu}{\mu} - \frac{E_{A\to A}(1-\mu)}{1 - E_{A\to A}(1-\mu)}\right)\\
&= \frac{E_{A\to D}P_{D\to 1}\mu}{1 - E_{A\to A}}\left(\frac{(1-\mu)(1 - E_{A\to A}(1-\mu)) - \mu E_{A\to A}(1-\mu)}{\mu(1 - E_{A\to A}(1-\mu))}\right)\\
&= \frac{E_{A\to D}P_{D\to 1}\mu(1 - \mu - E_{A\to A}(1-\mu))}{(1 - E_{A\to A})\mu(1 - E_{A\to A}(1-\mu))}\\
&= \frac{E_{A\to D}P_{D\to 1}(1-\mu)}{1 - E_{A\to A}(1-\mu)}
\end{aligned} \tag{33}$$

when $E_{A\to A}(1-\mu) < 1$ and the geometrical sums converge. Otherwise $R_0 = \infty$. This result is equal to the analytical result of R_0 in equation (18).

Table A1. Resident in virgin environment

ξ	$C(0) = 0,\ C(\xi) = A(\xi - 1)$	$\hat{F}(\xi)$
0	0	0
1	$D \cdot P_{D\to 1} = C(1)$	$C(1) \cdot E_{A\to D}$
2	$D \cdot P_{D\to 1} + C(1) \cdot E_{A\to A} = D \cdot P_{D\to 1}(1 + E_{A\to A})$	$C(2) \cdot E_{A\to D}$
3	$D \cdot P_{D\to 1} + C(2) \cdot E_{A\to A} = D \cdot P_{D\to 1}(1 + E_{A\to A} + E^2_{A\to A})$	$C(3) \cdot E_{A\to D}$
4	$D \cdot P_{D\to 1} + C(3) \cdot E_{A\to A} = D \cdot P_{D\to 1}(1 + E_{A\to A} + E^2_{A\to A} + E^3_{A\to A})$	$C(4) \cdot E_{A\to D}$
⋮	⋮	⋮