6 Metapopulations of Butterflies

Butterflies inhabit an unpredictable world. Consider the checkerspot butterfly, *Melitaea cinxia,* also known as the Glanville Fritillary. They depend on specific host plants for larval development. The population size is buffeted by the vagaries of weather, availability of suitable host plants, and random demographic stochasticity in the small patches. The result is that local populations often go extinct when the host plants fail, or when larvae are unable to complete development before the winter.

But butterflies also have wings. Even though the checkerspots are not particularly strong flyers (they move a maximum of a couple of kilometers and most individuals remain in their natal patch), butterflies occasionally move from one patch to another. Empty patches are eventually recolonized. So, over a regional scale the total number of butterflies remains nearly constant, despite the constant turnover of local populations.

Professor Ilkka Hanski and his students in Finland have been studying the patterns of extinction and recolonization of habitat patches by the checkerspot butterflies for two decades on the small island of Åland in southwestern Finland.

The butterflies on Åland can be described as a "metapopulation", or "population of populations", connected by migration. In the original formulation by Richard Levins, he imagined a case where each population was short-lived, and the persistence of the system depended on the re-colonization of empty patches by immigrants from other nearby source populations. Thus colonizations and extinctions operate in a dynamic balance that can maintain a species in the landscape of interconnected patches indefinitely.

Figure 6.2 Larvae of Melitaea cinxia feeding on plantain.

The Glanville Fritillary is a type of checkerspot butterfly, small orange-brown butterflies that are common in dry meadows. Its range extends over much of northern Europe. The larvae, spiny black caterpillars, rely almost exclusively on two host plants: *Plantago lanceolata* and *Veronica spicata*, both common weeds in dry meadows and rocky outcrops. They overwinter in webs close to the ground, and in the spring the adult butterflies emerge, feed on nectar, and search for suitable host plant on which to lay their eggs. The butterflies on Åland complete one generation per year.

Most organisms have a dispersal phase of their life cycle. What are the consequences of migration for the abundance and distribution of individuals in a local area? In the first few chapters we have only considered the dynamics of single, isolated, populations and have ignored any effects of migration. Now we will turn our attention to the effects of movement.

6.1 Start with the simplest model:

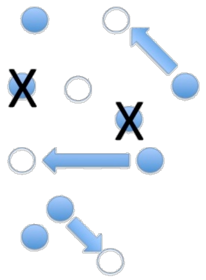
In order to focus our attention on migration we will focus only on the presence of absence of the species and ignore other aspects of population growth. Instead of keeping track of the number of individuals within each patch we will be concerned only with the proportion of occupied patches, *P*, which can vary from zero to 1.

The proportion of occupied patches will change by only two processes. The proportion of occupied patches will increase through colonization decrease through extinctions. So,

$$\frac{dP}{dt} = \text{Colonization rate} - \text{Extinction rate}$$

Already we can see that the system will be at equilibrium when colonizations exactly balance extinctions. But we still have not specified how colonization and extinction operate.

We will start by assuming that there are a large number of patches that are all identical. Each patch has an equal probability of going extinct in a particular time interval, and each occupied patch is equally likely to be a source of colonists for unoccupied patches. Therefore this simplest model assumes no spatial structuring of the landscape and no variation in the size or quality of the habitat patches.



How do we specify the colonization rate? The number of new colonizations will depend on the colonization rate, the proportion of occupied patches that can serve as a source of colonists, and the proportion of unoccupied patches.

There must be a source of colonists (probability =*P*) AND a colonization must occur (probability = *c*) AND there must be an empty patch to colonize (probability=(1-*P*)). If we assume those events are independent, then we multiply those probabilities. That means that colonizations will occur at a rate $cP(1-P)$. Extinctions will occur at a rate eP. That is the extinction rate per patch (e) times the probability that a patch is initially occupied (P).

Putting that all together we get:

$$\frac{dP}{dt} = cP(1-P) - eP \qquad \text{eq. 6.1}$$

To solve for the equilibrium, we set dP/dt=0 and get:

$$cP(1-P) = eP$$

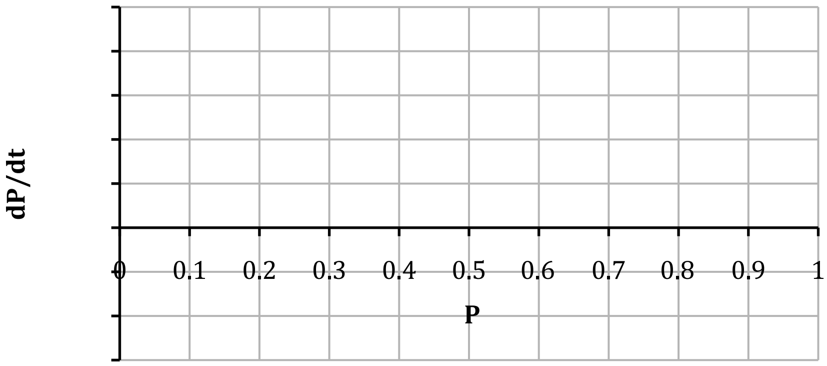
$$(1-P) = \frac{e}{c}$$

so the equilibrium is:

$$\hat{P} = 1 - \frac{e}{c} \qquad \text{eq.6.2}$$

At equilibrium, some of the patches will be occupied ($\hat{P} > 0$) as long as the colonization rate is greater than the extinction rate. The whole system is predicted to go extinct if $e \geq c$.

Is this equilibrium stable? Choose some value of *e* and *c* sketch a graph dP/dt vs. P. Will the system return to $\hat{P}$ when perturbed? *(Hint: Choose a few convenient points when sketching your graph: start with P=0, P=1 and P=* $\hat{P}$ *and think only about the sign of dP/dt rather than the exact value.)*



Notice that the criterion for a non-zero equilibrium patch occupancy is 1-e/c > 0 or c>e. What that means is that on average, each small population must colonize at least one empty habitat before it goes extinct. That is somewhat similar to our result from chapter 4 that the net replacement rate (R_0) of a population must be greater than 1.0 for the population to persist. If on average newborn females have less than one daughter before they die, then $R_0<1$ and the population will eventually decline to extinction.

6.2 Assumptions of the classical metapopulation model

- There is a large number of patches.
- Each patch has identical c and e rates. (all have equal probability of going extinct, all empty patches available to be colonized,
- the colonization rate is the same between any pair of patches).
- c and e are uncorrelated across patches
- We can ignore local population size and consider only the presence or absence of the species in a patch.

The metapopulation model is appropriate for systems with intermediate levels of migration between patches. If movement is extremely common then the system behaves as a single, larger, population. If migration is extremely rare, then each patch can properly be considered in isolation.

Why can the metapopulation persist? A key feature of the model is that we assume extinction events are all independent. Each local population is ephemeral, but the probability that all of the populations go extinct at the same time is vanishingly small. If the extinction probability of one patch is *e*, then the probability that two patches both go extinct is e_2 and the probability that all *k* populations go extinct simultaneously is e^k.

> Imagine a scenario where each local patch has a 50% probability of extinction each year. If there are 20 patches, what is the probability that *all 20* will go extinct in a given year?
>
> __________

Having many independent populations "spreads the risk" over the entire system. With a finite number of patches (small k), it is harder to maintain the metapopulation.

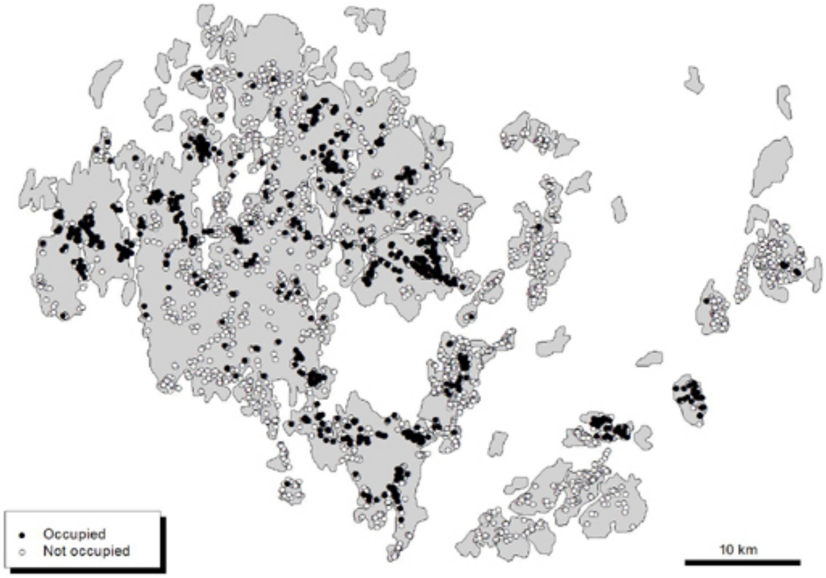
Similarly, if extinctions are correlated it will be difficult to maintain the metapopulation. If large-scale environmental changes are responsible for the extinction of patches, such that sets of nearby patches all go extinct together, then there may be no surviving populations to provide colonists. To the extent that extinction is correlated, the system will behave as if it were a single patch. Metapopulation persistence depends on the

6.3 Evidence that the checkerspots form a metapopulation

Does the species occur in discrete patches?

Hanski and colleagues have monitored the distribution and abundance of checkerspot butterflies on Åland by systematically observing patches of the host plants each summer and looking for the presence of caterpillars. The reliance on the host plant makes it possible to identify suitable habitats that could potentially be occupied, even when the butterfly is not present. They have identified over 3000 habitat patches that could potentially be occupied, of which only a few have checkerspots in any given year (Figure 6.3).

Figure 6.3 Occupied and unoccupied patches on the island of Åland in 2005 *(source: http://www.helsinki.fi/science/metapop/Field_sites/Åland.htm)*



Evidence of colonizations and extinctions

The metapopulation model assumes that there is a constant turnover of populations. Every year since 1991 Hanski and colleagues have returned to each patch and have recorded that presence or absence of checkerspots. As a result, they have a nearly complete record of occupancy and extinctions. Table 6.1 lists the results for 5 years of their census.

Table 6.1. Summary of metapopulation dynamics on Åland, 1993-1997.

Year	Occupied	Empty	Extinctions	Colonizations
1993	483	749		
1994	383	872	234	111
1995	356	926	155	106
1996	303	1026	170	101
1997	332	1146	131	142

(Source: Ehrlich and Hanski (2004) Table 4.2)

Taken together, we see that the butterflies occupy many small patches on the island, that at any point in time only a fraction of the possible sites are occupied, and that individual patches regularly go extinct or are re-colonized. Therefore these butterflies seem to fit the classical definition of a metapopulation.

6.4 What is the predicted patch occupancy rate of this metapopulation?

Using the data from table 6.1, calculate the average extinction and colonization rates of populations on Åland. The number of extinctions should be compared to the number of occupied sites *the previous year.* Similarly, the colonization rate should be calculated from the number of colonizations and the number of empty sites the previous year.

Year	Proportion occupied	Colonization rate	Extinction rate
1993	483/(483+749)=0.39	n/a	n/a
1994	0.30	111/749=0.15	234/483=0.48
1995	0.27	0.12	0.40
1996			
1997			

c=________________

e=________________

For your estimate of c and e, is what is the expected proportion of occupied patches at equilibrium? How does that compare to the average occupancy rate?

$\hat{P}$ =_______________

6.5 In a real system, distance between patches and size of the patch also matters.

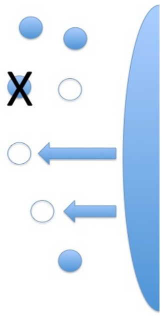
The simple metapopulation model did not do a good job of predicting the patch occupancy of these butterflies. The population surveys show more populations going extinct each year than are being colonized, and therefore predicts that the whole metapopulation should collapse. Although the occupancy rate is declining, there is still a high frequency of occupied patches. When our observations don't match the model predictions, it usually means that one or more of the model assumptions were violated.

What were the assumptions of the metapopulation model?

Which are most likely to be incorrect for these butterflies?

Our initial model was unrealistic in its assumption that all patches were identical in size and equally accessible to colonists. For example, in their surveys Hanski found that many of the patches contained only 1 or 2 larval groups. Those tiny populations were much more likely to go extinct than the large patches with population sizes over a thousand. What happens if we add some variation in the size of local populations?

Again we'll start with a very simple scenario. Imagine that there is one extremely large patch that serves as the source for all of the colonists. Call that the "continent" where the population is large enough that it will never go extinct. Then imagine that it is surrounded by small ephemeral populations ("islands") that go extinct at a rate e.



How will that affect the proportion of islands that are occupied? Again, dP/dt =colonizations – extinctions, but now the colonists all come from the large source population. How do we modify the equation to account for the large source? We still multiply the colonization rate times the frequency of empty patches, but we no longer need to include the frequency of occupied islands. All of the migration is assumed to come form the large continent, which we have assumed it always present. Therefore the colonization term is c(1-P). . Combining colonization and extinction we see that:

$$\frac{dP}{dt} = c(1-P) - eP \qquad \text{eq. 6.3}$$

At equilibrium,

$$\hat{P} = \frac{c}{c+e} \qquad \text{eq. 6.4}$$

In this model, can the island metapopulation go extinct?__________

Notice that with a mainland source, the island occupancy rate will never go to zero as long $c>0$. When there are a few large source populations that are resistant to extinction, then at least some of the islands are predicted to be occupied, as long as $c>0$.

In the case of the checkerspot butterflies on Åland, there is no single “mainland” population. But this example shows the general result that a network of small patches can persist in the face of high extinction rates, as long as there are other surrounding source populations. In addition, if there is some variation in patch size then large patches may be less prone to extinction. A few large and persistent populations can help to stabilize the entire metapopulation.

A second unrealistic feature of our first simple metapopulation model is that all islands are equally accessible. Checkerspot butterflies do not fly great distances. Hanski captured and marked hundreds of butterflies by writing a small number on the underside of their wing. When they later recaptured the butterflies, they found that almost all movement was between adjacent patches. None moved farther than 3 km. That means that the distance to nearby occupied patches probably has a larger effect on colonization rate than the total proportion of occupied patches in the entire metapopulation. Some potential patches are effectively unreachable if there are no occupied sites nearby.

There is a lot of current research developing more realistic metapopulation models that take spatial pattern into account. The basic approach is to modify the colonization and extinction rates so they become declining functions of isolation distance and patch size, respectively. The same conceptual approach holds, but now we substitute c^* and e^* for c and e.

More realism comes with a catch, however. We must now keep track of the explicit location of each patch, its distance from others, its size and potential for extinction. Those models are no longer easy to analyze so we must resort to computer simulations. Still, the results of that work with spatially explicit models generally support the main lessons from our simple models. They confirm that it is possible to maintain a species in a metapopulation even when there is a high probability of extinction for individual patches. The equilibrium patch occupancy is stable, and in principle the system could be maintained indefinitely in a dynamic balance between colonization and extinction. Variation in patch size (particularly large persistent populations that serve as a source of colonists) stabilizes the system even further.

6.6 **Your Turn:**

Collared Pikas (*Ochotona collaris*) are small mammals related to rabbits that live on talus slopes in the mountains of Alaska, the Yukon, and British Columbia. You can often hear the "peek" of their high-pitched call as they warn of the approach of a potential predator. The rocky talus slopes where they spend their time are separated by alpine meadows and form distinct habitat patches. Adults rarely stray from their patch. They harvest grass from the surrounding meadow and store it in large hay piles among the rocks for use during the winter months. The number of pikas in a particular talus patch is often small, so those individual patches have a high turnover through extinction and re-colonization.

Renee Franken and David Hik studied a pika metapopulation in the Yukon territory for several years. Using their data on the number of colonizations and extinctions of the patches, can you predict whether this metapopulation will persist?

Patch	**# years observed**	**# years occupied**	**Colon-izations**	**Extinct-tions**
cck	4	4	0	0
egh	7	7	2	1
snow	7	0	0	0
wo	7	6	1	1
gill	2	2	0	0
ws	7	5	0	1
ek9	7	7	0	0
wm	7	4	0	1
em8	7	6	4	1
ept	7	5	0	1
obl	2	2	1	1
haw	3	3	0	0
wpq2	7	5	1	1
wq17	4	0	0	0
wq12	7	0	0	1
whh3	4	0	0	0
ws3	7	5	0	1
ell4	3	2	1	1
ff7	4	4	0	1
wo3	7	6	2	1
wp9	7	0	1	0
enn4	3	2	1	1
kk0	2	1	1	0
ek5	7	6	4	1
ejj3	3	0	0	0
eii5	3	0	0	0
Total:	135	82	19	15

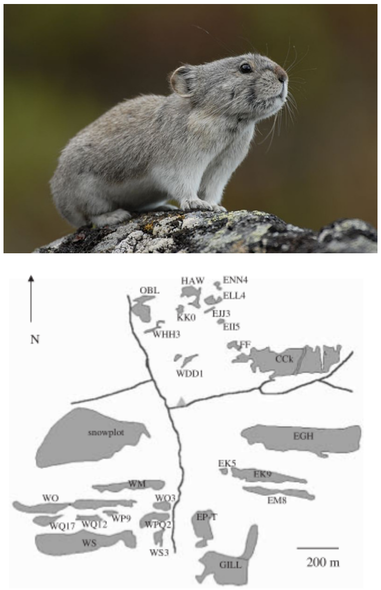


Figure 6.4. top: A collared pika. (source: http://farm2.static.flickr .com/1308/543563447_9582678214.jpg) Bottom; map of the Yukon study site. The shaded areas show the talus slope patches potentially occupied by pikas. (source: Franzen and Hik 2004 Fig. 1)

6.7 **Further reading:**

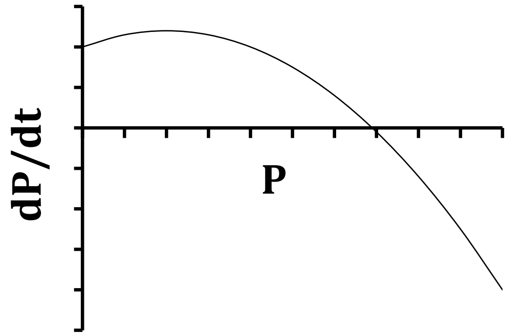
Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. pp 69-92 in I. Hanski and M. E. Gilpin, eds. *Metapopulation Biology*. Academic Press. San Diego.

Hanski, I. J. J. Hellmann, C.L. Boggs, and J. F. McLaughlin. 2004. Checkerspots as a model system in population biology. pp 245-263 in P. R. Ehrlich and I. Hanski, eds. *On the Wings of Checkerspots, a model system for population biology.* Oxford. New York.=

Franken, R. J. and D. S. Hik. 2004. Influence of habitat quality, patch size and connectivity on colonization ad extinction dynamics of collared pikas, Ochotona collaris. J. Animal Ecology 73: 889-896.

6.8 **Answers:** p. 3

the equilibrium (where dP/dt crosses the horizontal axis) is stable, providing c>e



p 4. Each patch has a 50% probability of extinction and there are 20 independent patches. $0.5^{20}=0.00000095$

p 5.

Year	p	c	e
1996	0.23	0.11	0.48
1997	0.22	0.14	0.43

The average colonization rate is 0.13 The average extinction rate is 0.45

$\hat{P}=1-\frac{e}{c}=1-\frac{0.45}{0.13}$ which is negative because e>c. That means the whole system is predicted to go extinct.

The average patch occupancy was 0.29, so they are clearly not extinct yet! There is, however, a trend for declining patch occupancy from 0.39 to 0.22.

p. 6. assumptions

As stated on p. 3, the main assumptions are that there are many identical patches with identical probabilities of colonization and extinction. Each patch is independent with regard to colonization and extinction. The assumptions most likely to be violated in a real system are the assumption of identical c and e across patches. In a real metapopulation, colonization is likely to depend on distance to source populations, and extinction is likely to depend on patch size or quality.

The island mainland metapopulation will not go extinct as long as c>0.

p. 8. Pikas.

You can get a rough estimate of the colonization and extinction rates by looking at the total number colonizations and extinctions observed, relative to the total number of "patch-years" in the study.

c=19/135 = 0.14

e=15/135 = 0.11

The equilibrium occupancy rate is predicted to be P=1-e/c = 0.21

The observed fraction of occupied patches (82/135=0.61) is substantially higher than predicted by the simple model. It is very likely that the real system has patches that differ in size (see map) and/or quality. So some patches may be less prone to extinction than others.