



# Effects of experimental population extinction for the spatial population dynamics of the butterfly *Parnassius smintheus*

Stephen F. Matter and Jens Roland

S. F. Matter (*mattersf@uc.edu*), Dept of Biological Sciences, Univ. of Cincinnati, Cincinnati, OH 45220, USA. – J. Roland, Dept of Biological Sciences, Univ. of Alberta, Edmonton, AB T5K 1X4, Canada.

While many studies have examined factors potentially impacting the rate of local population extinction, few experimental studies have examined the consequences of extinction for spatial population dynamics. Here we report results from a large-scale, long-term experiment examining the effects of local population extinction for the dynamics of surrounding populations. From 2001–2008 we removed all adult butterflies from two large, neighboring populations within a system of 17 subpopulations of the Rocky Mountain Apollo butterfly, *Parnassius smintheus*. Surrounding populations were monitored using individual, mark–recapture methods. We found that population removal decreased immigration to surrounding populations in proportion to their connectivity to the removed populations. Correspondingly, within-generation population abundance declined. Despite these effects, we saw little consistent impact between generations. The extinction rates of surrounding populations were unaffected and local population growth was not consistently reduced by the lack of immigration. The broader results show that immigration affects local abundance within generations, but dynamics are mediated by density-dependence within populations and by broader density-independent factors acting between generations. The loss of immigrants resulting from extinction has little impact on the persistence of local populations in this system.

No population can survive forever; extinction is the destiny of all populations. Many studies have examined factors influencing population extinction (Richter-Dyn and Goel 1972, Lande and Orzack 1988, Drake and Lodge 2004, Kramer et al. 2009); however, relatively little attention has been devoted to the effects of extinction for single-species spatial population dynamics. From a classic metapopulation perspective i.e. ignoring local population dynamics and focusing only on occupancy, the effects of extinction are relatively straightforward. Extinction opens a habitat patch for colonization and removes a potential source of colonists. Recolonization can occur if sufficient colonists remain, and metapopulations will persist when the rate of colonization exceeds the rate of extinction.

When considering the dynamics of local populations in population networks, the extinction of a local population can have multiple effects on the surrounding populations. The loss of a population should reduce the number of immigrants to surrounding populations. Importantly, this loss is not experienced equally for all surrounding populations, but should decrease with increasing isolation from the extinct population. Additionally the magnitude of immigrant loss will depend on the size of the population going extinct. Loss of immigrants is predicted to reduce population size in surrounding populations within generations. If immigration is important for local dynamics, we may also expect to see between generation effects on local extinction. Populations surrounding those undergoing extinction may have lower population growth rates due to reduced immigration. If local

populations are maintained by immigration (Pulliam 1988) the loss of immigrants may further result in local extinction for surrounding populations (Brown and Kodric-Brown 1977). Additionally, any reduction in abundance in the surrounding populations resulting from a local extinction in a nearby population should increase the risk of local extinction.

We build on previous work (Roland et al. 2000, Matter et al. 2004) and present results from a long-term, experimental study investigating the effects of local population loss for the spatial population dynamics of the Rocky Mountain Apollo butterfly *Parnassius smintheus*. Specifically we assess how the removal of two large, contiguous populations impacts the immigration, population size, growth and persistence of surrounding populations. We hypothesize that removal of these populations would reduce immigration to surrounding populations in proportion to their distance from the removals, resulting in lower population abundance and lower population growth rates. Additionally we were particularly interested in determining if small populations near the removals that had previously experienced extinctions would be affected by the loss of immigrants.

## Methods

### Study species

*Parnassius smintheus* (= *phoebus*) is an abundant butterfly in the Rocky Mountains of North America, although congeners

are threatened elsewhere. This butterfly feeds on several species of stonecrop throughout its range (Guppy and Shepard 2001). At our study site larvae are restricted to lance-leaved stonecrop *Sedum lanceolatum* and ledge stonecrop *Rhodiola integrifolia*. Although there is no preference or aversion for either species (Illerbrun and Matter unpubl.), *S. lanceolatum* sustains greater herbivory than *R. integrifolia* (<2%, Roslin et al. 2008). Both plants occur in gravelly sites above tree-line (Roslin et al. 2008). At our site, *P. smintheus* is the only herbivore of these species. *Sedum lanceolatum* produces the cyanoglucoside sarmentosin, which is present in all lifestages of the butterfly (Nishida and Rothschild 1995) and may afford larvae and adults protection from predation (Bohlin et al. 2008). Adults nectar on several yellow flowered species in the meadows. Nectar flowers can affect immigration (Matter and Roland 2002); however, natural levels of variation in floral abundance have little effect on abundance or dynamics (Matter and Roland 2010).

*Parnassius smintheus* is univoltine with a flight period from mid-July to September in our study area. Overwintering pharate larvae (first instar larvae still within the egg) hatch soon after snowmelt and begin feeding. Males fly more frequently and have a higher capture probability than females. Nonetheless, dispersal distances are similar for the sexes (Roland et al. 2000). Previous research with this species shows that dispersal is limited by forest habitat which imposes an edge effect (Ross et al. 2005) and decreases dispersal distance among meadows (Matter et al. 2004), affecting immigration rates (Roland et al. 2000), genetic structure (Keyghobadi et al. 2005), and local population dynamics (Roland and Matter 2007).

### Study site and population structure

Experiments were conducted in a network of 17 alpine meadows along Jumpingpound Ridge, Kananaskis, Alberta, Canada (Fig. 1, Table 1). Meadows are located above tree-line (~2200 m) and are bordered by forest consisting of lodgepole pine *Pinus contorta*; subalpine fir *Abies lasiocarpa*; and Engelmann spruce *Picea engelmannii*. Vegetation in the meadows is composed of grasses, sedges, mountain avens and numerous species of wildflowers including the butterfly's host and nectar plants (Ezzeddine and Matter 2008).

Study of this system began in 1995. Initially, meadows and butterfly subpopulations were somewhat arbitrarily assigned using forests and ridgelines as boundaries, then using the centroids of butterfly capture to determine subpopulation locations (Roland et al. 2000). These assumptions have proved to be valid. When defined in this manner, each meadow contains a semi-independent population with differing growth rates (Roland and Matter 2007) and genetic structure (Keyghobadi et al. 1999). The strength of the among-population correlation in growth and genetic structure is largely determined by distance between subpopulations that is comprised of forested habitat. Currently, all meadows and their subpopulations are separated by forest borders, but in some cases the borders are thin or incomplete (e.g. the border between meadows L and M is a patch of forest with openings to the east and west). The Jumpingpound system is isolated from other populations. The closest populations are located on Lusk Ridge, 6 km to the

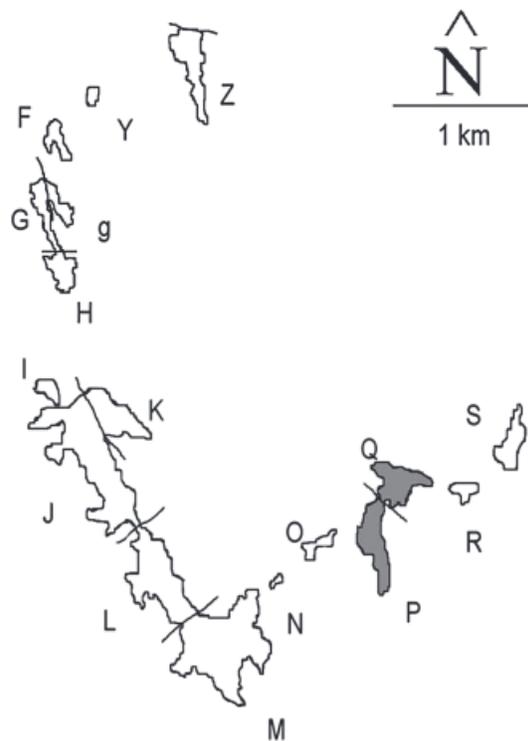


Figure 1. Study area showing populations of *P. smintheus* along Jumpingpound Ridge, Kananaskis Country, Alberta, Canada (50°57'N, 114°54'W). The 17 meadows and corresponding local populations are outlined. Bars between meadows indicate thin or incomplete tree-line which is a barrier to dispersal. The closest populations to Jumpingpound are meadows C–E on Lusk Ridge, 6 km northeast. Based on mark–recapture and genetic data they are isolated from Jumpingpound populations (Matter et al. 2004, Keyghobadi et al. 2005). Other meadows in this area (T–V, to the southeast of meadow S) do not contain the butterfly or its host plants. There are no meadows A, X or W. Meadow Z is separated from a large open area (not shown, Cox Hill), which periodically contains butterflies, but at a very low density due to few host plants. All butterflies were removed from P and Q (shaded) from 2001–2008, inclusive.

northwest and Powderface Ridge 10 km to the southeast. We have conducted simultaneous mark–recapture on these ridges over several years and have not observed movement among ridges. Genetic analyses also indicate little to no gene flow (Keyghobadi et al. 2005).

The Jumpingpound system functions along the continuum between a metapopulation and a patchy population (Hastings and Harrison 1994). Among-population dispersal is moderate, particularly for well connected populations; however, small, isolated populations experience extinction and recolonization.

### Experiments and general hypotheses

We used an experimental approach to investigate the effects of neighboring populations for the spatial population dynamics of *P. smintheus*. Beginning in 2001, we removed all butterflies (and some larvae) captured in meadows P and Q (Fig. 1), including immigrants from other meadows. Meadows were visited every 1–4 days over the entire flight season (weather permitting) and butterflies were captured by hand

Table 1. Characteristics of meadows and populations along Jumpingpound Ridge. Areas were determined from GPS collected in 2003. We show mean abundance (n) from 1995–2000 and 2001–2008, the years prior to and during removals of populations P and Q, and the mean observed emigration (E) rates prior to removal (1995 and 1996). To illustrate the effect of loss of populations in meadows P and Q, we show connectivity (S) in 2006 including the effect of meadows P and Q versus connectivity assuming abundance in P and Q is zero. Meadows P and Q were not included in analyses of the effects of their removal. Reductions in immigration and abundance in are predicted to be proportional to the change in connectivity. Connectivity changes with changing abundance among meadows, each year.

Meadow	Area (ha)	n (1995–2000)	n (2001–2008)	E/yr	Sw/P and Q	Swo/P and Q
F	3.1	69.9	57.0	3.5	0.88	0.88
G	2.5	157.0	99.0	14.5	1.69	1.69
G	2.2	110.7	80.2	10.5	1.30	1.30
H	2.3	56.7	36.2	7.0	1.11	1.11
I	1.2	59.3	65.4	0.0	1.77	1.77
J	16.1	102.1	170.2	3.0	2.32	2.31
K	7.3	82.8	105.4	1.5	2.15	2.14
L	8.9	194.6	200.5	3.0	2.02	1.96
M	22.7	154.6	282.1	2.5	2.22	2.06
N	0.2	7.7	3.0	0.5	2.07	1.25
O	3.4	24.5	54.9	1.5	3.13	0.36
P	6.6	97.9	314.2	3.5	3.76	0.31
Q	5.3	84.2	253.8	5.0	3.75	0.21
R	0.4	6.4	14.5	0.0	2.09	0.07
S	4.7	14.2	22.2	0.5	0.37	0.06
Y	0.8	7.3	7.7	0.5	0.49	0.49
Z	7.1	93.8	134.1	0.0	0.02	0.02

netting. The purpose of the removals was not necessarily to cause the actual extinction of these populations, but to minimize the immigrant pool to other meadows, simulating their extinction in terms of spatial population dynamics. We suspected that the loss of these populations would impact surrounding populations given the relatively high number of observed emigrants, population size, and contribution to connectivity (Table 1).

The predicted loss of immigrants should affect surrounding populations in proportion to their connectivity to the removals. Thus, each surrounding population will be affected differently. If immigration is an important component of population size, we expected the abundance of butterflies in meadows affected by the removals to decrease. Again, the reduction in abundance due to the loss of immigrants should be proportional to the reduction in their connectivity resulting from the removals.

Populations in small meadows have low abundance and are periodically observed to have no adult butterflies. Prior to removals (1995–2000) no adult butterflies were observed in one year for populations in meadows N (1995), S (2000) and Y (1996), and for three years in meadow R (1998–2000). If these populations are maintained by immigration we expected the number of extinctions to increase relative to pre-removal conditions, in particular for populations in meadows N, R and S. Similarly, we would expect population growth to be low in these populations.

### Mark–recapture and population estimates

We used mark–recapture techniques to evaluate the effects of the removals. We censused meadows three to six times during the adult flight periods during the summers of 1995–1996 and from 2001–2008. We captured butterflies using hand nets and each was given a unique 3-letter mark on its hind wings. For all captures, we recorded the date, location (based on x, y coordinates from aerial photographs), sex and identity. Location is accurate to ~ 20 m (Roland et al.

2000). We used Craig’s method to estimate population size in each meadow during each census period (Craig 1953). The frequency of butterflies captured once, twice, thrice, etc. is assumed to follow a Poisson distribution. The zero term of the distribution, the number not caught, is estimated and added to the number caught to arrive at a point estimate of population size. In general, we continue capturing until about 75% of captures are daily recaptures which produces high accuracy for this estimate (Craig 1953). This method is more accurate than capture–recapture methods that do not account for multiple captures within a census (Matter and Roland 2004). We used the maximal abundance observed each year as our estimate of population size in each meadow. We adopted this method because of differing phenologies among meadows and differences in the number and timing of censuses.

From 1997–2000 (and to 2002 for meadows I, J and K), we estimated population size in each meadow using transect counts (Pollard 1977). Here, each observer walked a path through the middle (along the longest axis) and around the circumference of a meadow tallying the number of butterflies observed at any distance in front of them. As these butterflies fly more frequently when it is sunny (Ross et al. 2005), we only conducted transect surveys during full sun. For each survey there were between two and four observers, and meadows were surveyed 2–3 times each year. To arrive at a population estimate for each survey, we calculated the mean number of butterflies reported by the observers and converted it to a ‘common currency’ of population size as estimated by Craig’s method via a regression equation relating the two metrics (Matter and Roland 2004).

The number of immigrants to each population was enumerated each year in which individual mark–recapture occurred. We define an immigrant as a marked butterfly arriving in a different meadow than it was previously observed. This method clearly underestimates the actual number of immigrants, but is unbiased after controlling for the number of times a meadow was censused.

We defined a local extinction as the observation of no adult butterflies in a meadow during normal mark-recapture and the observation of no larval feeding scars on host plants. For the latter, we sampled 15–200 randomly placed 1.69 m<sup>2</sup> quadrats per meadow. Sampling occurred past the peak of the adult flight season each year, after which most larval activity had ended. The number of quadrats sampled per meadow was scaled to its area. Within each quadrat we determined the number of host plants and any evidence of feeding damage characteristic of *P. smintheus*.

### Landscape data and connectivity

We determined the area (ha) and location of each meadow in ARC View 5.1 using differentially corrected GPS data collected in 2003. We measured distances between populations based on the centroids of butterfly capture (Roland et al. 2000). Using digitized aerial photographs taken in 1993, we determined the distances between populations comprised of forested and open habitat. We measured distance along the spine of the ridge as these butterflies rarely cross valleys (Roland et al. 2000).

To examine how each population (*j*) surrounding the population removals would be affected, we used the best fit connectivity (*S*) metric and parameters:

$$S_{j(t)} = A_j^{0.93} \sum_{k \neq j} \exp(-4.47d_{fjk} - 1.83d_{mjk}) 0.04A_{k(t)}^{-0.23} N_{k(t)}$$

where *A* is meadow area, *N* is population abundance, and *d<sub>f</sub>* and *d<sub>m</sub>* are the distance between the source *k* and target *j* meadow comprised of forest and open habitat, respectively. We arrived at this model by comparing AIC<sub>C</sub> for connectivity models with different assumptions (i.e. models including or not including target area) to immigration data from 1995 and 1996 (Matter unpubl).

We estimated parameters by fitting the virtual migration model to combined mark-recapture data from 1995 and 1996 (Hanski et al. 2000, Matter et al. 2004). We note that connectivity changes based on the abundance in each population, each year. This metric differs from Matter et al. (2005) where total geometric distance, rather than distance along the ridge comprised of forest and meadow habitat, was used to allow comparison to another system.

### Effects of local extinction on surrounding populations

To estimate the effects of removals, we compared the connectivity metric either assuming that populations *P* and *Q* were extinct, i.e. abundance of zero, or were at their nominal abundance. We note that our removals in no way resulted in the complete ‘extinction’ of these populations; however the constant removals should make the effects of *P* and *Q* for surrounding populations more consistent with them being extinct than being extant at their nominally observed abundance. We estimated the nominal population size in meadows *P* and *Q* using a similar procedure as for abundance in other meadows. We determined the maximum number of butterflies removed (captured) on any single date. We

then converted these captures to abundance as estimated by Craig’s method using the known relationship between these two estimates (Matter and Roland 2002). This method likely underestimates the population sizes for *P* and *Q* relative to other populations, because elsewhere butterflies can survive between censuses increasing the estimate. Thus, this is a conservative estimate of the effects of their loss for other populations.

We expected that if the removals affected surrounding populations, models not including *P* and *Q* would show a better fit than models including them. A reduction in connectivity implies a reduction in immigration. Because the model not including *P* and *Q* will always predict fewer immigrants than the model assuming that there are extant populations in these meadows, a better fit by the extinction model also indicates a reduction in immigration (abundance or growth) that is proportional to the reduction in connectivity.

We examined the effects of population removal on the number of immigrants by comparing statistical models first incorporating the number of times a meadow was censused each year. Then we added either the connectivity metric including or excluding meadows *P* and *Q*. To avoid bias due to butterflies not being individually marked in meadows *I*, *J* and *K* in 2001 and 2002, we restricted our analysis of immigration to period 2003–2008. Because the number of immigrants consists of count data, we used generalized linear models assuming a Poisson error distribution and a log link function (McCullagh and Nelder 1989). We corrected for overdispersion using a quasi-Poisson distribution with estimated dispersion for significance tests. Because there was the same number of parameters for each model we compared the deviance explained.

To evaluate the effects of population removals on abundance, we used a similar procedure. We compared the fit of connectivity models to the maximum observed abundance in each meadow, each year from 2001–2006. For the abundance models we assumed a Gaussian error distribution and an identity link function (McCullagh and Nelder 1989). Abundance was square root transformed to improve linearity.

The between generation effects of population removal was evaluated by examining the population growth rates in relation to connectivity. We calculated growth rates as  $r = \ln((N_{t+1} + 0.5)/(N_t + 0.5))$ . We added one half an individual to all abundances to account for populations going extinct during the study. Use of other values (e.g. +1) did not quantitatively change the results. Growth from year *t* to *t* + 1 was related to connectivity in year *t*.

To determine the effects of population removals on extinction we tallied the number of apparent (no butterflies observed) and confirmed extinctions (no butterflies and no larval feeding damage). Here the expectation is that both apparent and confirmed extinctions should increase as a result of population removals. We compared the yearly rate for each population prior to and during population removals.

## Results

From 2001 to 2008 we made 15 499 captures of 8025 individual butterflies along Jumpingpound Ridge; a mean of 1.93 captures per individual. Over this time we removed 4830 butterflies from meadows *P* and *Q* (Fig. 2). We observed

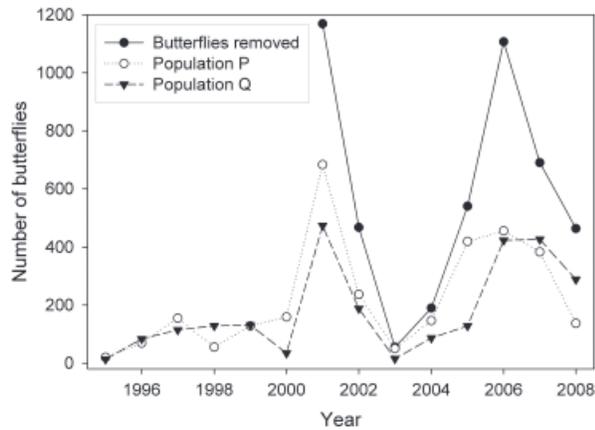


Figure 2. The combined number of *P. sintheus* removed from meadows P and Q each year during the experiment. A total of 4830 butterflies were removed by hand-netting beginning in 2001 and ending in 2008. Also shown are the yearly estimated maximum population sizes for populations in meadows P and Q. These population sizes are not directly comparable as number of butterflies removed is across the entire flight season. When calculating abundance in P and Q during removals, we used the maximum number of butterflies removed per day and converted it to population size as estimated by Craig's method (Matter and Roland 2004).

558 between meadow dispersal events from 2003 to 2008. In 2003 there was a ridge-wide population crash; only 93 individuals were observed in 2003, excluding removals. The crash appears to have resulted from overwintering mortality. Mating success evidenced by the presence of a sphragis (Calabrese et al. 2008) was normal in 2002 (81% mated females in 2002 vs a mean of 86% in previous years (1995, 1996, 2001), but larval feeding decreased substantially from 2002 to 2003 (32% reduction in the percentage of damaged rosettes), indicating overwintering mortality. Mortality likely resulted from larvae experiencing temperatures below their supercooling point ( $-30^{\circ}\text{C}$ , Matter and R. Lee unpubl.) due to lack of snow cover.

Based on the connectivity metric and abundances observed during the removal period, we predicted reductions in connectivity, and thus immigration, ranging from 0.0 to 97% (Meadow R in 2007). Based on this model the spatial extent of the removals should extend from P and Q east to S, a mean 75.9% reduction, and to L to the northwest, a mean 2.4% reduction. The population in J, the next closest meadow to the removals was predicted to have a mean 0.4% reduction, and more distant populations to the north of J should have been virtually unaffected by the removals (Table 1).

Fitting statistical models with connectivity terms either including or excluding P and Q showed that the removal reduced the number of immigrants to surrounding meadows (Fig. 3). The statistical model using the connectivity term not including meadows P and Q as a source of immigrants (i.e. assuming  $n=0$ ) showed a significant increase in immigrants to each meadow (2003–2008) as connectivity increased; the model including the nominal abundance of butterflies in P and Q was not significantly related to immigration (Table 2). These results indicate that the removals reduced immigration to surrounding populations in proportion to their connectivity to

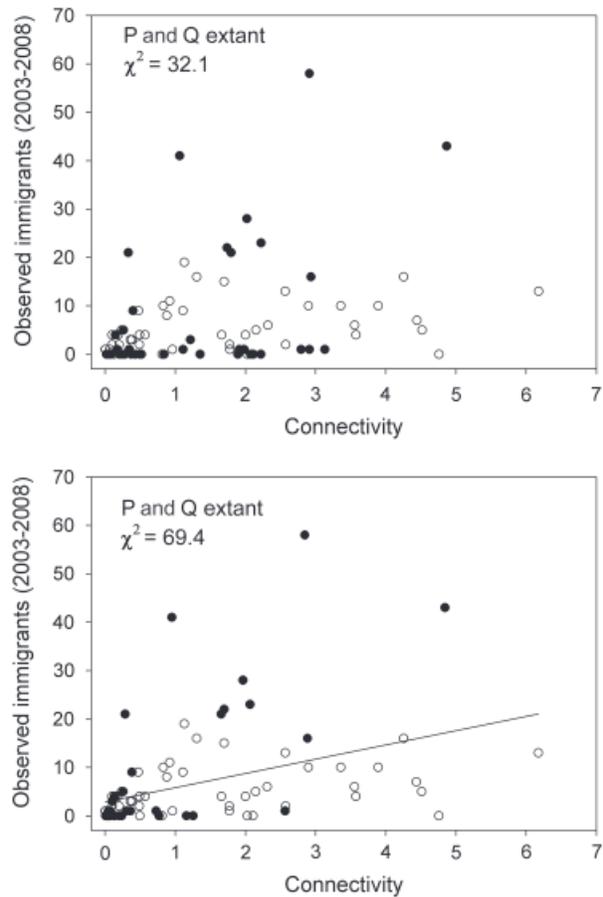


Figure 3. Effects of the removal of populations P and Q for the observed number of immigrants to surrounding populations. The top figure shows the relationship assuming that populations in P and Q were extant and contributed to connectivity. The bottom panel shows the relationship assuming extinction in P and Q, and thus not contributing to connectivity. A Poisson regression model showed that a connectivity metric assuming extinction in meadows P and Q fit the observed number of immigrants better than did a model including the effects of P and Q (Table 3). These results indicate that population removals reduced immigration to surrounding populations in proportion to their connectivity to the removal meadows. Statistical models also included the methodological factor, the number of times a population was censused. Filled circles indicate populations where connectivity was predicted to be most reduced by the removals (L, M, N, O, R and S). In comparing panels, note that many of these populations had few immigrants and were moved near the origin when connectivity was calculated without P and Q.

P and Q. For both models, the observed number of immigrants increased with the number of censuses per meadow (Table 2).

Local abundance in surrounding populations was reduced as a result of the removals (Fig. 4). Local population abundances from 2001–2008 were more strongly related to the connectivity metric excluding P and Q than to the metric including them at their nominal abundance (Table 2), indicating that the population removals reduced abundance in relation to their connectivity to the removals. Both models showed a significant relationship to local population abundance, but the connectivity metric excluding P and Q showed a better fit than did the connectivity metric assuming that P and Q were at their nominal abundance.

Table 2. Analysis of deviance table showing the effects of population removal for immigration/census and abundance in surrounding populations. Significance tests for immigration are based on quasi-Poisson distributions and estimated dispersion ( $\phi$ ). Abundance used a Gaussian distribution and was square-root transformed.

	DF	Deviance	B ( $\pm$ SE)	F	p	$\phi$
Immigration						
Null	89	1035.0				
Intercept			0.33 $\pm$ 0.27	8.8		
Censuses	1	333.0	0.25 $\pm$ 0.05	37.8	< 0.01	
Connectivity with P and Q	1	32.1	0.17 $\pm$ 0.09	3.6	0.06	
Intercept			0.37 $\pm$ 0.26			8.6
Censuses	1	333.0	0.23 $\pm$ 0.04	39.0	< 0.01	
Connectivity without P and Q1		69.4	0.04 $\pm$ 0.01	8.1	< 0.01	
Abundance						
Null		119	3644.8			
Intercept			4.04 $\pm$ 0.61			20.3
Connectivity with P and Q	1	1255.7	2.46 $\pm$ 0.31	62.0	< 0.01	
Intercept			4.40 $\pm$ 0.53			18.1
Connectivity without P and Q1		1514.0	2.71 $\pm$ 0.29	83.8	< 0.01	

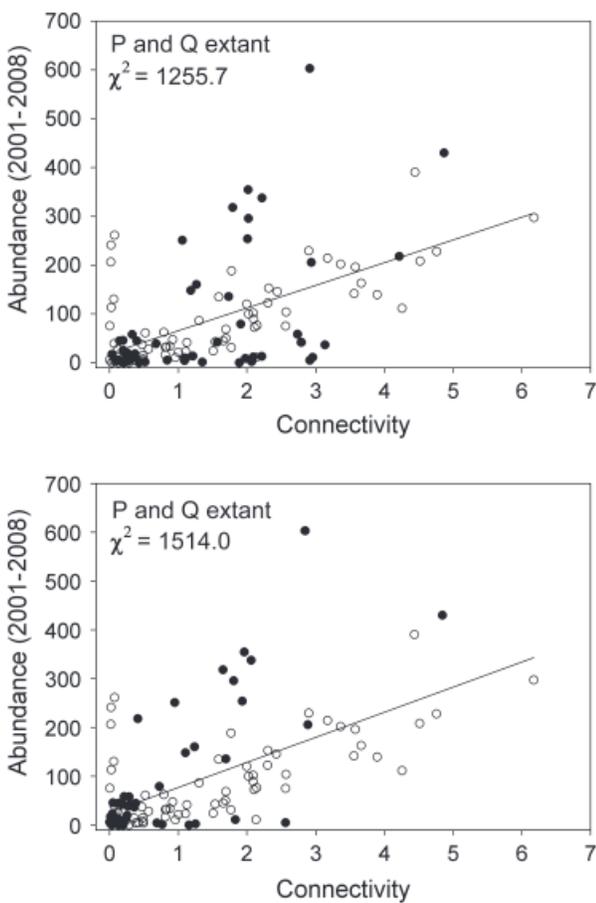


Figure 4. Effects of population removals for local abundance. The top panel shows the relationship between abundance and connectivity including the abundance of populations in meadows P and Q. The bottom panel shows connectivity assuming extinction of populations in meadows P and Q. Both connectivity metrics showed significant relationships with abundance, however the model using the connectivity metric excluding meadows P and Q showed a better fit than the model including them (deviance explained 1255.7 vs 1514.0) indicating that the removals reduced abundance in surrounding meadows in proportion to their connectivity to the removals. Filled circles indicate populations where connectivity was predicted to be most reduced by the removals (L, M, N, O, R and S).

Despite the within-generation reductions in immigration and abundance resulting from the removals, there were only marginal between-generation effects. Initial inspection of the relationship between population growth and connectivity indicated that there was greater variation in growth for less connected population than for well connected populations (Fig. 5); a result largely due to the fact that the connectivity is lower for populations in small meadows, which are smaller and have inherently greater variation. Neither connectivity model showed a significant relationship to population growth. Violation of the assumption of homoskedasticity would lead us to reject the null hypothesis more often than warranted, thus finding no relationship would not be improved by accounting for this violation. Local population growth showed significant variation among years ( $F_{6,98} = 27.2$ ,  $p > 0.01$ ). After accounting for this source of variability, there were no significant relationships between local growth and either connectivity metric ( $F_{1,97} = 0.01$ ,  $p = 0.92$  (model excluding P and Q);  $F_{1,97} = 0.38$ ,  $p = 0.54$  (model including P and Q)). We also found no significant interactions between year and either connectivity metric ( $F_{6,91} = 1.53$ ,  $p = 0.18$  (excluding P and Q);  $F_{6,91} = 0.53$ ,  $p = 0.79$  (including P and Q)). When examining only small populations near the removal (N, O, R, S), where immigrants would be expected to have the largest per capita impact on growth, we again found no effects of connectivity or the extinction of local populations on the growth of surrounding populations ( $F_{1,26} = 0.33$ ,  $p = 0.57$  (excluding P and Q);  $F_{1,26} = 1.16$ ,  $p = 0.29$  (including P and Q)).

During the eight years of population removal (2001 to 2008) there were six observations of no adult butterflies over an adult flight season – Y in 2003 and 2004, in N in 2003, 2004 and 2007; and in K in 2003. For all of these apparent extinctions we found evidence of larval feeding damage, except for meadow N in 2004. For the six years prior to the removals (1995–2000) there were also six observations of no adult butterflies. Examination of larval feeding damage did not begin until 2002 thus direct comparison of actual extinction cannot be made. However either assuming the same actual to apparent extinction rate for earlier data, or simply examining apparent extinction, the rate was higher prior to population removals than during the removals.

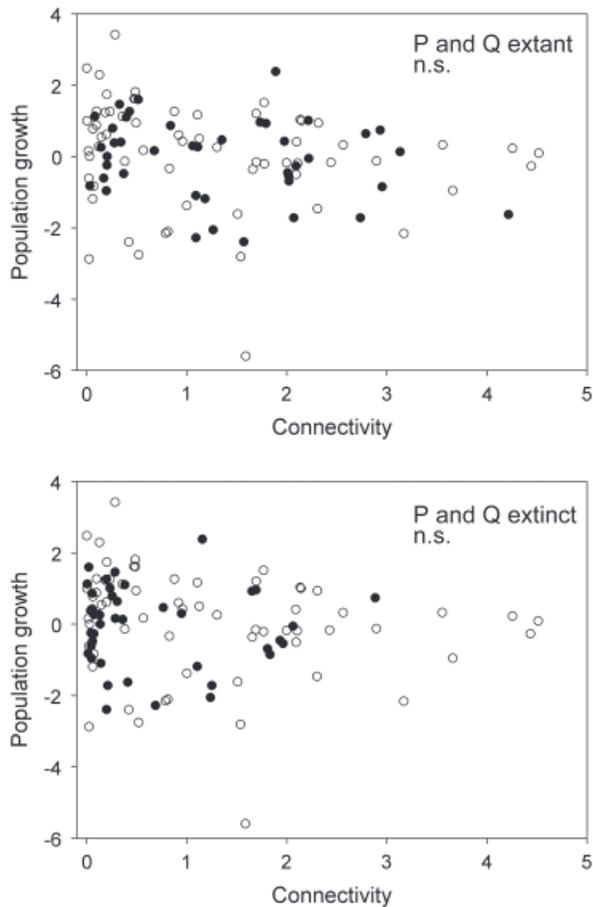


Figure 5. Effects of population removals on local population growth. The top panel shows the relationship between growth and connectivity including the abundance of populations in meadows P and Q in the calculation of connectivity. The bottom panel shows connectivity assuming extinction of populations in meadows P and Q. Neither model showed a significant relationship to local growth (P and Q extant:  $F_{1,103} = 3.88$ ,  $p = 0.06$ ; P and Q extinct:  $F_{1,103} = 1.88$ ,  $p = 0.17$ ). We note that significance tests here are too liberal due to violation of the assumption of homoskedasticity. Models including year (Results) also showed no significant relationships. Filled circles indicate populations where connectivity was predicted to be most reduced by removals (L, M, N, O, R and S).

There is also no difference if we assume consecutive years of apparent extinction represent a single extinction event. Thus, population removals did not increase local extinction. Populations undergoing apparent extinction during the population removal period had significantly lower connectivity (assuming no effect of P and Q) than did extant populations (0.32 vs 1.24; separate variance  $t = 4.34$ ,  $DF = 11.64$ ,  $p > 0.01$ ; Levene's test of equality of variance  $F_{1,118} = 6.06$ ,  $p = 0.01$ ), indicating that, in general, reduced immigration may promote extinction despite the fact that the reduction in immigration resulting from local population extinction did not.

## Discussion

Our large-scale, long-term experiment validated several hypotheses for spatial population ecology that previously

had been untested in natural systems. Experimental extinction of local populations resulted in decreased immigration to surrounding populations. Importantly from both ecological and experimental design perspectives (Steinberg and Kareiva 1997), local extinction did not affect surrounding populations equally; the effect of removal on immigration to surrounding populations decreased with increasing isolation from the removals. Within-generations the loss of immigrants resulted in a reduction in abundance for surrounding populations, again in proportion to isolation from the extinctions.

Despite the effects for immigration and abundance, our experimental results failed to confirm expectations regarding extinction risk. Contrary to expectations (Richter-Dyn and Goel 1972, Brown and Kodric-Brown 1977, Pulliam 1988) neither the loss of immigrants themselves nor the reduction in local abundance in surrounding populations resulted in higher rates of local population extinction. The lack of an effect likely arises because the magnitude of reduction in immigrants and abundance from the treatment extinction was insufficient to cause extinction in surrounding populations, rather than any general refutation of the processes thought to increase extinction risk. This result was somewhat surprising given that the mean abundances of populations N and R prior to the experimental removals were both less than eight individuals and they had experienced extinctions prior to the experimental removals. We anticipated that even a small reduction in immigration would increase their risk of extinction. Demonstrating the predicted effects of local extinction for surrounding populations in spatial networks may be difficult. Our experiment lasted for eight years, thus any increase in extinction risk should have been detectable, especially given the population crash in 2003 and the attendant low population sizes across the system. The crash did result in local extinctions, but it was followed by three years of increasing population sizes, possibly affecting results. Overall, our results indicate that the loss of immigrants and attendant reduction in abundance resulting from local population extinction in this system are not sufficient to increase the risk of extinction for surrounding populations.

Results of this study help to address the long standing question in ecology of how spatial processes affect temporal population dynamics. The *Parnassius* system appears to be governed largely by between-generation processes; dispersal among populations within a generation increases local abundance, but this increase in abundance does not necessarily increase growth. Across all populations there was no consistent relationship between connectivity and the direction of population growth, and this relationship did not change with experimental extinction, i.e. immigration neither consistently bolsters nor diminishes population growth. This result does not mean that immigration does not affect temporal dynamics; rather it shows how immigration interacts with density-dependent and density-independent factors operating in this system. Across all populations density-independent factors related to weather are highly important (Roland and Matter unpubl.). Density-dependent factors related to host plant defense or quality also appear to play a role (Roslin et al. 2008). In such a system, immigration may increase growth if density-dependent factors are weak and decrease growth when they are strong. The overall effect of

dispersal on growth in this system depends on a combination of density independent and dependent factors within populations. Continuing research is examining these questions.

The importance of between generation processes is reinforced by the removals themselves. Despite the considerable reduction in the migrant pool caused by our removals, as evidenced by the modeling results, the dynamics of populations P and Q largely mirrored those across the rest of the ridge. Based on our recapture rate, the lifespan and fecundity of females, and removal intensity, we estimate that we reduced the potential reproductive output in these populations by over 75%. That the dynamics mirrored populations along the ridge, illustrates the effects of correlated meso-scale factors such as weather (Matter and Roland 2010). While we did not investigate larval survival during the removals, the fact that constant intense removal did not result in a proportional reduction in abundance indicates a release from density-dependent factors.

There are few other studies with which to directly compare our results. Experimental and non-experimental studies of habitat fragmentation are numerous (reviewed by Debinski and Holt 2000), however these studies are almost always confounded by having both population loss and habitat loss, rather than just population loss. The best demonstration of the effects of local population extinction in a spatial system comes from a natural experiment involving the butterfly *Euphydryas editha* (Thomas et al. 1996). These butterflies live on two host plants within rocky outcrops and on a novel host plant within forest clear-cuts. Population growth rates of the butterfly are substantially higher in the clear-cuts than in the outcrops and migration is asymmetrical from clear-cuts to outcrops. A rare summer frost killed all host plants within the clear-cuts, but not in the outcrops, and consequently population size in the outcrops fell by two thirds. Immigrants from the clear-cuts made up a significant fraction of the outcrop populations, but populations in the outcrops were not extinction-prone. Similar to our results, dispersal merely added to population sizes in the outcrops rather than rescuing them from extinction.

We have made progress toward understanding why local population extinctions occur, but we are only beginning to understand their effects for spatial population dynamics. The results of our study suggest that the impacts can be minimal, primarily affecting the abundance of surrounding populations within generations. An important caveat regarding our experiment is that it is unreplicated at the metapopulation scale. Thus, our results run the risk of being idiosyncratic. Further investigation of the effects of extinction within spatial population networks is needed to reach any generalization.

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