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Predicting immigration of two species in contrasting landscapes: effects of scale, patch size and isolation

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Migration is a key process for spatially structured populations. We examined how a variety of patch based metrics commonly used to predict the number of immigrants to a habitat patch performed based on data from three different years, in two distinct insect systems. The first system was an herbivorous beetle inhabiting patches of its host plant within a 'typical' patch network. In this system there were numerous patches located relatively close to one another, given the beetle's dispersal ability. The second system consisted of a butterfly inhabiting a series of 17 subalpine meadows. Here, the patches were arranged in a linear fashion and were more distant from each other. Overall, we found that the best models incorporating aspects of patch size and/or isolation explained a large (30–40%) amount of deviance in immigration, but there were considerable differences between the systems. For the first system, we found that metrics including the size of the target patch explained the highest proportion of deviance in immigrant numbers, while metrics based only on interpatch distances explained very little deviance. The situation was reversed for the second system. Metrics including the size of the target patch explained little deviance, while metrics based on the distance between patches explained the bulk of deviance in the number of immigrants. The results of our study show that the effects of patch size and isolation on the number of immigrants are highly important, but dependent on spatial scale, the organism studied, and how it responds to the spatial arrangement of patches. Correspondingly, there will be no single generalized metric to predict immigration for all cases. Given the dependency of the results on the system studied, we recommend that future studies provide explicit data on habitat areas and dispersal distance relative to interpatch distance to allow for meaningful comparison among organisms and systems.

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Immigration is a fundamental process for spatially structured populations that affects dynamics at both local and regional scales. Understanding and predicting population dynamics hinges on understanding the amount and pattern of movement among populations (Sutcliffe et al. 1997, Hanski 1999). In situations where movement among populations is infrequent, the dynamics of local populations will be largely independent of other populations, barring spatially correlated environmental factors. On the other hand, if movement among populations is very frequent, 'populations' simply will be spatially referenced parts of one large population, all with synchronous dynamics.

Building on island biogeographic theory (MacArthur and Wilson 1967), spatial population ecology and metapopulation dynamics have related immigration (or

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colonization) to two main patch-based factors – habitat area and isolation. The number of immigrants that a particular site receives is expected to decrease with increasing isolation and to increase with increasing area (Hanski 1994). Although numerous studies have shown that habitat area and isolation are important factors affecting immigration and spatial population and community patterns (MacArthur and Wilson 1967, Simberloff 1976, Connor and McCoy 1979, Matter 1996, Sutcliffe et al. 1997, Hanski 1999), the quantification of these factors has varied.

Habitat area is relatively straightforward in its measure. Generally it is defined as the geometric area of a particular habitat type or the amount of a key resource such as host plants for an herbivorous insect. Subtle, but important, differences between these approaches can arise if resources are not proportional to habitat area (Matter et al. 2003). Regarding habitat isolation, we have come to little consensus on how best to describe it. In its simplest form, isolation may be thought of as the distance between a habitat patch and the nearest patch of the same type of habitat, i.e. nearest neighbor or island–mainland distances. Such formulations ignore contributions from other populations in the landscape (Hanski 1999). Thus, alternative metrics often incorporate the distance to all patches within a landscape or within some prescribed area.

Ideally, a metric of isolation will be functional rather than simply a geographic or geometric abstraction, in that it describes a species' response to habitat structure (Tischendorf and Fahrig 2000, Moilanen and Hanski 2001). In terms of population ecology, this functional definition equates to describing immigration. A patch of habitat that receives more immigrants than another patch is less isolated, no matter how distant it is in terms of meters or kilometers. That metrics of isolation need to be species-specific simply reflects the diversity in dispersal ability and distances seen in nature (Hanski and Kuussaari 1995). Connectivity metrics (sensu Hanski 1994) attempt to describe the isolation of a habitat patch for a particular species by reflecting the number of immigrants that it receives. As such these metrics usually include interpatch distance scaled by a species' dispersal ability, and can incorporate other factors affecting immigration such as the sizes of the emigrant pool and focal habitat patch.

Here, we compare the performance of several general metrics used to predict the number of immigrants in patchy landscapes. Because of a lack of good dispersal data for spatial systems (Bowne and Bowers 2004), previous examinations have either used simulated data (Bender et al. 2003) or have focused largely on colonization using presence–absence data (Moilanen and Nieminen 2002). The present study uses multiple years of high quality spatial mark–recapture data for two insect species within their distinctive landscapes. Specifically, we test the hypothesis that a single, generalized metric will consistently be the best predictor of the number of immigrants.

Methods

This study uses two empirical data sets. The first system is an herbivorous beetle inhabiting patches of its host plant at a relatively small spatial scale. The second system is a butterfly inhabiting sub-alpine meadows at a broader spatial scale.

Study species

The natural history of the red milkweed beetle, *Tetraopes tetraophthalmus* (Forster), has been described in detail elsewhere (Chemsak 1963, Matter et al. 1999). Salient features for this study are that the beetle is a univoltine, monophagous herbivore of common milkweed, *Asclepias syriaca*. Female beetles can be distinguished by the presence of a suture on the ventral surface of the last segment that is absent in males (Chemsak 1963). *Asclepias syriaca* is a clonal perennial, commonly found in pastures and old-fields in eastern North America. Its clonal nature results in a heterogeneous distribution with patches consisting of one individual (genet) ranging in size from one to several hundred ramets.

The second species examined was the Rocky Mountain Apollo butterfly, *Parnassius smintheus* Doubleday. This butterfly is abundant in sub-alpine meadows in the Rocky Mountains. Its larval host plant, lance-leaved stonecrop, *Sedum lanceolatum* Torr., occurs in gravelly sites above tree-line (Fownes and Roland 2002). Adults require nectar resources, and typically feed on yellow-flowered species such as *S. lanceolatum*, alpine goldenrod (*Solidago multiradiata*), and black-tipped groundsel (*Senecio lugens*) found throughout the meadows. *Parnassius smintheus* is univoltine with a flight period from mid-July to mid-August in our study area. This species is sexually dimorphic with males having a white to yellow ground color. Females are darker and more translucent due to a lower density of wing scales. In the field, adult males are more apparent than the relatively sedentary females. Nonetheless, estimated dispersal distances are equal between the sexes (Roland et al. 2000).

Study sites and mark–recapture

Tetraopes tetraophthalmus

Mark–recapture was conducted in a 40 ha meadow at the University of Virginia's Blandy Experimental Farm, Boyce, Virginia (Clarke County) USA. The meadow consists primarily of bedstraw (*Galium verum*), honeysuckle (*Lonicera japonica*), several grasses (*Festuca* and *Poa* spp.), and patches of common milkweed. The meadow was pastured prior to 1983 and was burned or mowed, approximately every other year between 1984 and 1995, to reduce the number of woody plants.

All milkweed patches (defined as a ramet separated by <10 m from other ramets) were identified and censused for beetles during the summers of 1992 and 1995–97. New patches established during the study were also defined as a ramet or group of ramets separated by over 10 m from the nearest ramet. Due to the growth of patches, some interpatch distances declined to less than 10 m during the study. We used the number of ramets as a metric of patch size as it explains more variation in beetle abundance than does geometric area (Matter 1997). The number of ramets in each patch was counted each year. The location of the center of each milkweed patch was estimated in 1992 using a transit and existing grid system within the farm. Patch locations in other years were determined using a handheld GPS with differential correction (±1 m accuracy).

We searched for beetles daily over the first two weeks of adult activity and approximately three times a week thereafter. Each newly captured beetle was given a unique mark on its elytra using model enamel (Matter 1996). The sex, date, and location were recorded for all beetles captured. Only previously marked beetles arriving from a different patch were scored as immigrants. Because all patches were censused frequently and an equal number of times, this method should provide an unbiased estimate of the number of immigrants, although it is likely an underestimate. Population size within each patch was estimated as minimum number known alive (Matter 1997).

Parnassius smintheus

Mark–recapture of *P. smintheus* was conducted in a network of 17 meadows located above tree-line (~2100 m) along Jumpingpound Ridge, Kananaskis, Alberta, Canada. Because meadows contain both larval and adult resources, host and nectar plants; each meadow was considered a habitat patch. For consistency with Roland et al. (2000), different parts of very large meadows were delineated as separate meadows. Meadows are comprised of grasses, sedges, and wildflowers, and are bordered on their lower slopes by forest consisting of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelman spruce (*Picea engelmannii*). The area (ha) and location of each meadow was determined in ARC View 5.1 using differentially corrected GPS data collected in 2003. To allow direct comparison with the *Tetraopes*-*Asclepias* system, the distance (km) between meadows was measured from the center of each meadow, rather than along the ridge (Roland et al. 2000, Matter et al. 2003, 2004). Butterflies in each meadow were censused three to five times over roughly five-week periods in 1995, 1996, 2001 and 2002. We captured butterflies using hand nets, giving each a unique three letter mark on both hind wings. For all captures, we recorded the date, location, sex and identity mark. To equilibrate effort among meadows, recapture continued until approximately 75% of butterflies had been previously captured that day.

In 2001, we began a large-scale experiment involving the removal of two populations on one end of the ridge. Based on data from 1995 and 1996 (Matter et al. 2004), the loss of these populations should affect only populations on the southern end of the ridge and not those on the central and northern parts of the ridge. Thus for 2001 and 2002, we limit our investigation of immigration to the six northernmost meadows. Isolation metrics for these years were calculated considering all meadows. We estimated meadow-specific population sizes each year using Craig's method (Craig 1953, Roland et al. 2000). Intensive mark–recapture was not conducted in three meadows in 2001 and 2002. Instead, population sizes were estimated using a transect method and converted to a 'common currency' of population size as estimated by Craig's method via a regression equation (Matter and Roland 2004).

Metrics

We examined how well several metrics commonly used in spatial population studies explain variation in the number of immigrants to a patch (see Moilanen and Nieminen 2002 and Bender et al. 2003 for a general discussion of some of these isolation metrics). Under a passive sampling scenario, the number of immigrants is assumed to be proportional to habitat area (Connor and McCoy 1979). Thus, the first metric we considered was patch size. For brevity, this metric is henceforth abbreviated as PA. The second metric was nearest-neighbor distance, which was simply calculated as the linear distance from a patch to the closest patch (henceforth NN; Hargis et al. 1998, Välimäki and Itämies 2003). The third metric was the summed distance from a patch to all other patches in the landscape (CD; Matter 1996, Välimäki and Itämies 2003). The fourth metric was Voronoi polygon area (VA) which is calculated as the area of a polygon defined by the midpoints between a patch and all other patches in the landscape (Bender et al. 2003). We calculated VA using the minimum convex polygon routine of the program CALHOME (Kie et al. 1996). Finally, we considered a series of increasingly complex connectivity models (sensu Hanski 1994). Connectivity here is considered as a patch-based metric rather than an overall landscape metric (Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001; see Hargis et al. 1998 for an examination of some landscape metrics). Connectivity conceptually can be thought of as the inverse of isolation. The first connectivity metric (C1) was a summed exponentially decreasing function of the distance between patches:

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij})$$

where S_i is the connectivity of patch i, d_{ij} is the distance between patch i and j, and α is a species-specific parameter describing the inverse of mean migration distance (Hanski 1994, 1999). The next connectivity metric (C2) takes into account the potential number of emigrants produced by all other populations by using patch size (A_j) as a proxy for population size (Hanski 1999):

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) \eta A_j^{-\zeta_{em}} N_j$$

The species-specific parameters η and ζ_{em} describe the rate of emigration from a patch of unit size (1 ha or ramet) and the scaling of emigration with patch size, respectively. Note that the parameters η and ζ_{em} derived from the virtual migration (VM) model (Hanski et al. 2000) describe the probability of an individual emigrating. Thus to estimate the number of emigrants produced by a patch, the value is multiplied by population size N_j. Because the previous method uses area as a surrogate for population size, but population data was available, we also used a metric (C3) based on the population size of all surrounding populations:

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) \eta N_j^{-\zeta_{em}} N_j$$

where N_j is population size for patch j (Hokit et al. 1999). The final connectivity metric (C4) accounts for the size of the patch to which individuals immigrate and scales immigration with patch size:

$$S_i = A_i^{\zeta_{im}} \sum_{i \neq j} \exp(-\alpha d_{ij}) \eta A_j^{-\zeta_{em}} N_j$$

where ζ_{im} is a parameter scaling the number of immigrants with the size of the target patch (Moilanen and Nieminen 2002).

All parameters for connectivity metrics were estimated using the VM model (Hanski et al. 2000, Matter et al. 2004). Each parameter for each species was calculated assuming the conditions of the respective connectivity model (e.g. for C1, only α was estimated, all patches were considered to be of unit size, and patch-size based emigration and immigration were discounted). To obtain parameter estimates as independent of the data being modeled as possible, we used mark–recapture data collected at the same sites but in different years: in 1992 for *Tetraopes* (Matter 1996, 1997) and in 1995 for *Parnassius* (Roland et al. 2000, Matter et al. 2004). For each species, these years represent the only other available data. As previous research has shown differences in the movement of male and female *T. tetraophthalmus* (Lawrence 1982), we calculated separate parameters for each sex (Table 1). For *P. smintheus*, we combined data on males and females due to the low recapture rate for females and similar dispersal patterns (Roland et al. 2000). All metrics, except C3, were calculated both considering all patches and only occupied patches (metrics using only occupied patches were abbreviated with an O, e.g. NNO). This method was adopted because the occupancy status of a patch is rarely known with certainty and the possibility exists that unoccupied patches may facilitate dispersal (Roslin and Koivunen 2001). A patch was considered to be occupied if at least one individual was observed there within a year.

Statistical methods

The number of immigrants was modeled using a generalized linear model. Because the dependent variable (number of immigrants) was a count, we assumed Poisson-distributed errors and a log link function (McCullagh and Nelder 1989). Each metric was evaluated independently. We used the proportion of deviance explained to assess the explanatory power of each isolation metric. To control for the effects of sampling effort on the number of immigrating butterflies recorded, we entered into the model the number of times a meadow was censused each year before assessing the effects of isolation metrics. To examine the relationships among isolation metrics we calculated Pearson's moment product correlation. Correlations were calculated between each metric for each system, each year.

Results

We captured a total of 8600 individuals (5305 *Tetraopes* and 3295 *Parnassius* individuals) and recorded 3208 migration events (3070 for *Tetraopes* and 138 for *Parnassius*, Table 2). For the *Tetraopes* system, the number of milkweed patches and their size increased during the study (Table 2). Correspondingly, the metrics also varied over the study. As more and larger patches appeared, the mean isolation of individual patches decreased.

Different isolation metrics provided different descriptions of the spatial setting. In general, metrics were correlated with each other, but several pairs showed only weak correlations (for simplicity only results for male *Tetraopes* in 1997 are depicted, Fig. 1). In particular, connectivity metrics incorporating the size of the target patch (C4 and C4O) failed to show strong correlations with metrics that did not incorporate the size of the

Table 1. A summary of parameters used for connectivity metrics. All parameters were fitted using the VM model (Hanski et al. 2000) with data from 1992 and 1995 for *Tetraopes* and *Parnassius*, respectively. Note that parameter estimates are dependent on the model used.

Metric	*Tetraopes tetraophthalmus*			*Parnassius smintheus*
	Parameter	Male	Female	
C1	α	33.03	39.21	4.29
C1O	α	34.44	40.45	3.05
C2	α	7.69	8.53	2.03
C2	η	0.01	0.01	0.02
C2	ζ_{em}	0.44	0.34	0.10
C2O	α	7.42	8.20	2.05
C2O	η	0.01	0.01	0.05
C2O	ζ_{em}	0.18	0.30	0.27
C3	α	8.51	8.61	2.41
C3	η	0.01	0.01	0.07
C3	ζ_{em}	0.57	0.43	0.00
C4	α	6.37	7.72	2.42
C4	η	0.03	0.02	0.02
C4	ζ_{em}	0.22	0.20	0.12
C4	ζ_{im}	0.86	0.74	2.59
C4O	α	6.41	7.57	2.27
C4O	η	0.03	0.03	0.07
C4O	ζ_{em}	0.22	0.19	0.12
C4O	ζ_{im}	0.81	0.66	2.58

target patch. Nearest neighbor metrics and VA also showed relatively weak correlations with connectivity metrics. Because of the loose correlations among several metrics, we expect a priori that they should vary in their ability to predict the number of immigrants.

There were striking differences between the systems in the proportion of deviance explained by the metrics (Fig. 2, 3). For both sexes of *T. tetraophthalmus*, in all years, the size of the target patch was exceedingly important in explaining the number of immigrants (Fig. 2). Target patch size and connectivity metrics that incorporated target patch size explained 13–46% of deviance in immigration, whereas metrics not including target patch size explained $<7\%$. For *P. smintheus*, metrics including the size of the target patch explained the least deviation ($<3\%$, Fig. 3) and distance-based metrics explained the greatest amount of deviation in the number of immigrants, generally 30–40%.

For *T. tetraophthalmus*, C4O explained the greatest proportion of deviance in immigration in all cases. Voronoi area explained only a minimal amount of deviance ($<6\%$). As shown previously (Matter 1996), there were differences between the sexes. Isolation metrics explained slightly more, and metrics with target patch size slightly less deviance in immigration for female beetles than they did for male beetles.

For *P. smintheus*, in 2000 and 2001, the simplest connectivity metric, assuming only an exponentially decreasing dispersal distance (C1), explained the largest proportion of deviance. In 1996, the distance to the nearest occupied patch (NNO) explained the largest proportion of deviance. Voronoi area generally explained less deviance than did distance based metrics and slightly more than metrics using the area of target meadows. There was no consistent trend between metrics using all patches or only occupied patches.

Discussion

Our examination of the immigration of *Parnassius* and *Tetraopes* focused on two key patch characteristics, size and isolation. For both of these systems it is known that specific factors such as matrix habitat, habitat quality, and sex ratio affect dispersal (Lawrence 1988, Roland et al. 2000, Matter and Roland 2002). Thus, it was somewhat surprising that size and isolation alone performed so well. Overall, these two spatial attributes of patches explained a considerable amount of deviation

Table 2. A summary of some characteristics for each system. Data shown are mean values across all patches (±1 sd, where applicable). Note that the *Tetraopes-Asclepias* system consists of a varying number of habitat patches each year. Isolation metrics were not calculated for years in which connectivity parameters were derived.

Tetraopes-Asclepias	1992	1995	1996	1997
Individuals (male; female)	676; 708	462; 526	748; 774	694; 717
Immigrations (male; female)	237; 189	218; 235	676; 470	654; 391
Number of patches	61	75	87	97
Patch size (ramets)	14.1 (±19.4)	21.4 (±41.0)	24.7 (±39.0)	37.5 (±62.9)
Nearest neighbor (m)		22.2 (±16.9)	18.0 (±14.4)	18.0 (±12.9)
Cumulative distance (km)		15.8 (±3.2)	18.3 (±3.9)	20.3 (±4.4)
Voronoi area (m^2)		36209 (±339)	37007 (±194)	37950 (±202)
Male connectivity (C1)		11.1 (±3.7)	13.2 (±4.4)	12.8 (±4.4)
Male connectivity (C1O)		8.8 (±3.1)	10.9 (±3.9)	9.2 (±3.3)
Parnassius smintheus	1995	1996	2001	2002
Individuals	579	587	1142	987
Immigrations	17	25	40	56
Number of meadows	17	17	17	17
Meadow size (ha)	5.6 (± 5.9)	5.6 (± 5.9)	5.6 (± 5.9)	5.6 (± 5.9)
Nearest neighbor (m)		386.1 (±151.7)	386.1 (±151.7)	386.1 (±151.7)
Cumulative distance (km)		32.2 (±4.5)	32.2 (±4.5)	32.2 (±4.5)
Voronoi area (ha)		170.7 (± 7.3)	170.7 (± 7.3)	170.7 (± 7.3)
Connectivity (C1)		0.43 (±0.27)	0.43 (±0.27)	0.43 (±0.27)
Connectivity (C1O)		0.74 (±0.34)	0.74 (±0.34)	0.74 (±0.34)

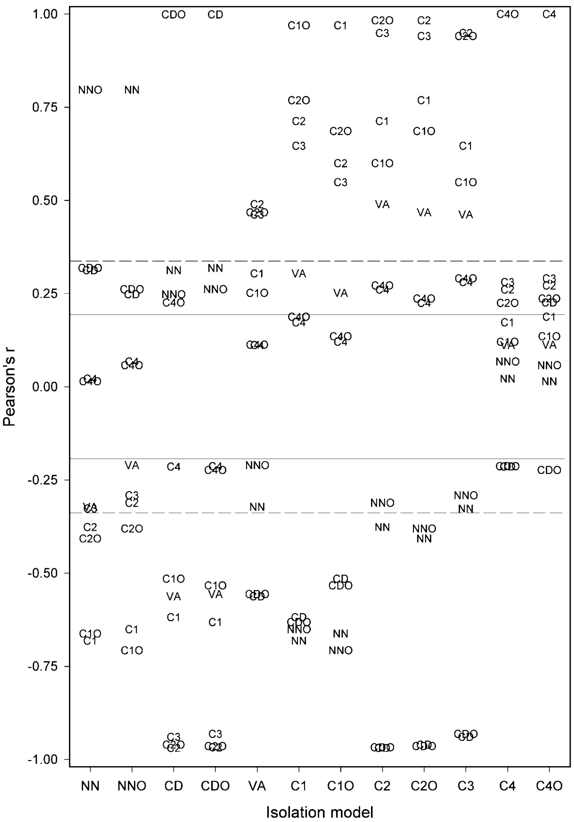

Fig. 1. Pearson's moment product correlation (r) among different isolation metrics calculated for male *Tetraopes tetraophthalmus* in 1997. Abbreviations for each metric are plotted at the value of r for the correlation between the metric in question and that indicated on the x axis. For all values of r, n = 97 patches. The horizontal bars show the critical value of r ($P < 0.05$) before (solid line) and after (dotted line) Bonferroni correction for 65 tests.

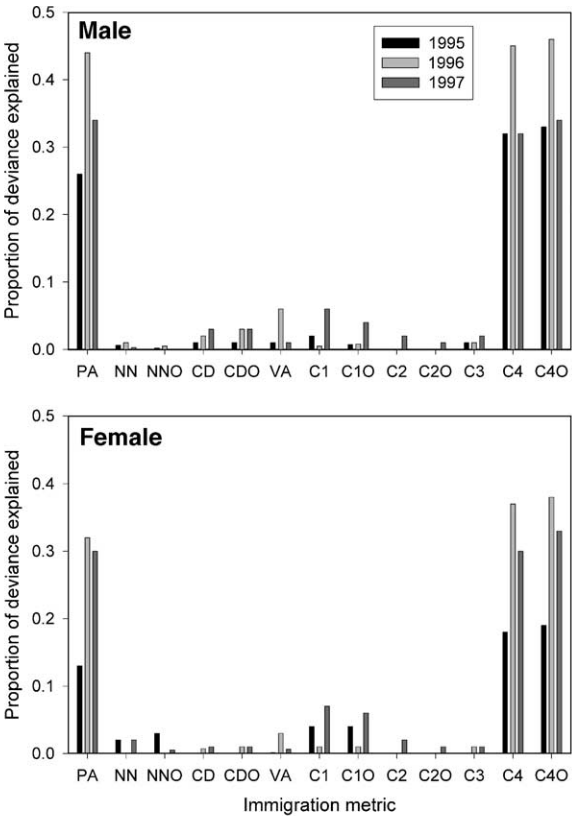

Fig. 2. The proportion of deviance in the immigration of *Tetraopes tetraophthalmus* to patches of *Asclepias syriaca* explained by each metric. See text for an explanation of metrics and abbreviations.

in immigration (30–40%) indicating the general importance of these factors for spatially structured populations.

The differences observed between the two study systems provide important insights regarding immigration in patchy landscapes. For both systems, the spatial attributes of individual habitat patches explained a large proportion of deviation in the number of immigrants. Yet, for *T. tetraophthalmus*, the size of the target patch was highly important and patch isolation was relatively unimportant. For *P. smintheus*, the situation was reversed; meadow isolation was paramount and the size of the target patch was inconsequential. These differences may reflect differences in taxa and landscapes, but are more likely a combination of interspecific differences in dispersal ability relative to the spatial scale of the systems. *Parnassius smintheus* must disperse farther between patches than *T. tetraophthalmus*, as illustrated by differences in the values of α estimated for each system (Table 1). If the frequency of dispersal decreases exponentially with distance, $1/\alpha$ corresponds to the mean migration distance. Thus, estimated interpatch migration distances are 25–147 and 233–493 m for *Tetraopes* and *Parnassius*, respectively, using the highest and lowest estimates of α (Table 1). These estimates of migration distance are a function of dispersal ability and interpatch distances (Porter and Dooley 1993, Matter 1996), which were much shorter for *Tetraopes* than for *Parnassius*. The mean nearest neighbor distance was 18 m in the *Tetraopes* landscape and 386 m in the *Parnassius* landscape (Table 2). Despite the short observed mean migration distance, *Tetraopes tetraophthalmus* is a strong flier (Davis 1981). The frequency of dispersal distance for *T. tetraophthalmus* decreases with distance; however movements of over 400 m are not uncommon (Fig. 4 in Matter 1996), and this species has been shown to colonize patches 5.5 km from the nearest patch (McCauley 1989). In contrast to *Tetraopes*, the dispersal ability of *Parnassius* is more limited. Roland et al. (2000) examined the dispersal of *P. smintheus* both within and between patches and found that the mean migration distance was only 143 m. Thus, at the scales of our study, interpatch distances relative to dispersal ability are

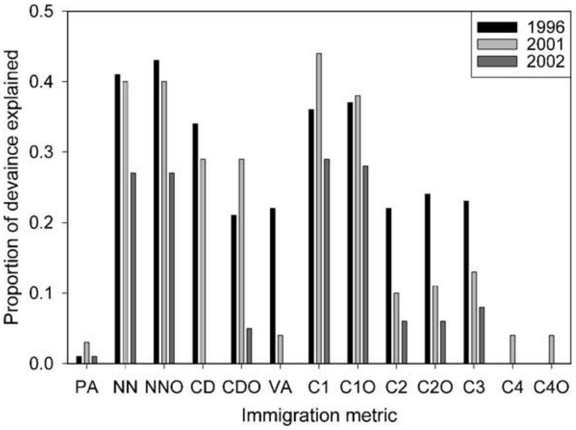

Fig. 3. The proportion of deviance in the immigration of *Parnassius smintheus* to sub alpine meadows explained by each metric. See text for an explanation of metrics and abbreviations. Deviance was estimated after accounting for the number of times a patch was censused in a year. Immigration was evaluated for 17 meadows in 1997 and six meadows in 2001 and 2002.

greater for *P. smintheus* than for *T. tetraophthalmus*, resulting in a greater importance of patch isolation for the immigration of *P. smintheus* than for *T. tetraophthalmus*.

The importance of spatial scale with respect to the dispersal ability of the target species is also illustrated by a comparison of our results for *P. smintheus* to a study of the clouded Apollo, *Parnassius mnemosyne* by Välimäki and Itämies (2003). They examined the importance of target patch size and four isolation metrics. These two congeneric species could be assumed to have similar dispersal capacity, but Välimäki and Itämies (2003) found that target patch size and population density in the target patch explained the greatest amount of variation in male immigration. The regression model best explaining female immigration included these same two factors and the distance to the nearest occupied patch, but the variance explained by the distance to the nearest occupied patch was much lower than for density and area (Välimäki and Itämies 2003). This incongruity with our results on *P. smintheus* can be explained by the large difference in the spatial arrangement of the two systems: Välimäki and Itämies's (2003) study contained 58 patches with a mean nearest occupied patch of 118 m. Hence, their system was more like the *Tetraopes* system than that of *P. smintheus.* Correspondingly, patch isolation played a smaller role.

Differences in the relative importance of patch size between the *Tetraopes* and the *Parnassius* systems may be a function of the spatial configuration of patches. For *Tetraopes* patches are arranged as a network, where, for most patches other patches can be found in any direction. For *Parnassius*, meadows occur in a linear fashion along a horseshoe-shaped ridge, where the closest meadow is usually found by traversing along the ridge-top. In linear systems, patches are encountered by dispersers primarily from two sides, rather than in proportion to perimeter or area as in a typical network. Thus, the linear arrangement of meadows for *Parnassius* may preclude the 'patch as a target' analogy often used to explain the positive relationship between immigration and area (Connor and McCoy 1979, Sutcliffe et al. 1997). The linear arrangement of meadows may also explain the poor fit of Voronoi area for this data.

Although patch size was highly important for *Tetraopes,* a passive sampling hypothesis where the number of immigrants is directly proportional to patch size, does not hold. The scaling of the intensity of immigration (number per unit patch size) with patch size for *Tetraopes* is significantly less than one (Matter 1997). Thus, while the number of immigrants increases with patch size, the number of immigrants per unit patch size is greater for smaller patches than for larger patches. Despite the differences between the *Tetraopes* and *Parnassius* systems, *Parnassius* shows the same response as *Tetraopes*- proportionately greater immigration to smaller patches (Table 1). For *Parnassius*, this pattern holds whether using the amount of resources (number of *Sedum* plants) or meadow area, as each explains nearly equal amounts of variation in immigration (Matter et al. 2003). Sutcliffe et al. (1997) suggested that this pattern of area-dependent dispersal may be common.

Among the different descriptors of isolation, connectivity metrics generally performed better than other isolation metrics. This result should not be surprising, given that connectivity metrics are specifically designed to predict immigration. However, there are important caveats regarding the use of connectivity metrics (Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001). One particular warning illustrated by this study is that more complicated connectivity metrics do not guarantee better results. The most complicated metric (C4) did perform well for *T. tetraophthalmus*, but not for *P. smintheus*, where less complicated metrics explained the greatest proportion of deviance. On the other hand, there are many factors beyond patch size and isolation that affect immigration (Lawrence 1988, Peterson 1997, Pither and Taylor 1998, Roland et al. 2000). Given the profound impact of the spatial setting and geometry of patches shown here, examining the effects of these basic spatial attributes is a general starting point before discriminating more refined factors affecting dispersal in specific landscapes, such as habitat quality or matrix habitat (Roland et al. 2000, Matter and Roland 2002, Matter et al. 2004).

The results of our research clearly show that there is no single metric that will best predict immigration for every system, and as the *Parnassius* data demonstrate, the best metric may not even be consistent within the same system. To some degree this result was anticipated by Hanski et al. (1994), who explored several isolation metrics in their study of the butterfly *Melitaea cinxia*. The lack of a consistent metric between systems warns against indiscriminate application of isolation metrics to predict or model immigration. However, due to correlations among most metrics within a system, the important question to consider seems to be whether to include target patch size or not. Including target patch size where it is unimportant – or not including patch size where it is important – can drastically reduce predictive ability. The performance of any isolation metric will depend on spatial context, the species considered, and how each species responds to the particular spatial context. For these reasons, to allow for meaningful comparison, future studies of dispersal in patchy landscapes should explicitly include information detailing patch sizes and dispersal distance relative to interpatch distance.

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