Am. Midl. Nat. 150:26–36

The Effects of Isolation, Habitat Area and Resources on the Abundance, Density and Movement of the Butterfly Parnassius smintheus

STEPHEN F. MATTER[1]
Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221

AND

JENS ROLAND, NUSHA KEYGHOBADI[2] AND KRIS SABOURIN
Department of Biological Sciences, University of Alberta, Edmonton, Canada T6G 2E9

ABSTRACT.—We examined the effects of isolation and site size on the abundance, density, emigration and immigration of the butterfly *Parnassius smintheus* in a series of sub-alpine meadows. Site size was measured either as habitat area or as number of host plants within each meadow. This distinction allowed us to test the hypothesis that population density measured over area (a generalized individuals-area relationship) should tend to decrease with increasing area due to inclusion of more 'non-habitat' in larger areas. In general, area measured either as meadow area or host plant abundance explained little deviance in butterfly abundance or movement. Immigration increased with the connectivity (the inverse of isolation) of meadows. We found that individuals-area relationships defined over meadow area showed patterns of decreasing butterfly density with increasing meadow area. This pattern was partially generated by a trend for host plant density to decrease with increasing meadow area. However, this trend was not universal as some small meadows had similar host plant densities to large meadows. Decreasing density with increasing meadow area primarily arose due to decreasing butterfly density with increasing host plant abundance, indicating that multiple mechanisms can produce decreasing population density with increasing area.

INTRODUCTION

A common premise in ecological studies is that population size, immigration and emigration are related to the size and isolation of sites (MacArthur and Wilson, 1967; Simberloff, 1976; Connor and McCoy, 1979; Hanski, 1999). The abundance of individuals is assumed to increase proportionately with habitat area (Haila, 1988; Bowers and Matter, 1997). If organisms arrive at sites randomly, larger areas represent larger targets and should receive more immigrants than smaller areas (Connor and McCoy, 1979; Lomolino, 1990). The number of emigrants is also expected to increase with area, as it should increase with population size. Isolation is expected to affect immigration, with more isolated sites receiving fewer immigrants (Matter, 1996; Hanski, 1999; Moilanen and Nieminen, 2002), and may affect abundance if immigrants make up a large fraction of the population. These relationships with site area and isolation form the basis for much of biogeographic, metapopulation, and spatial population theory.

An important consideration in population and community ecology is how density and the

---

[1] Corresponding author: Telephone (513) 556-9713; FAX (513) 556-5299; e-mail: mattersf@email.uc.edu

[2] Present address: The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103

rates of emigration and immigration vary with site size. The relationship between density and site size is often referred to as the individuals-area relationship (Schoener, 1986; Connor *et al.*, 2000) or the density-area relationship (Matter, 1997, 2000). Understanding how population density relates to habitat size underlies basic ecological theory and is pertinent to conservation issues (Haila, 1988; Bender *et al.*, 1998; Gaston *et al.*, 1999; Connor *et al.*, 2000; Matter, 2000). From a phenomenological perspective, the individuals-area relationship affects single-species population and metapopulation dynamics as well as community patterns. Within a network of habitat patches, increasing or decreasing density with area clusters individuals into large or small patches, respectively. This clustering changes the relative importance of different sized patches and alters predictions of metapopulation dynamics and community patterns (Matter, 2000, 2001).

Recently, Gaston and Matter (2002) proposed that individuals-area relationships may depend on how, and the scale over which, the relationship is defined. Connor *et al.* (2000) showed that local population density generally increases with site area within systems of naturally and experimentally created habitat patches (patch-based individuals-area relationships or PIARs, in the terminology of Gaston and Matter, 2002). Studies at this scale typically use estimates that are closer to 'ecological density', *i.e.*, site size is defined by a resource (Elton, 1933). In contrast, studies without reference to habitat type or resources, usually conducted at broader spatial scales (generalized individuals-area relationships or GIARs), show that density tends to decrease with increasing area as an inverse power function (Smallwood and Schonewald, 1996; Gaston and Blackburn, 2000). Here, estimates of density are usually 'crude' rather than ecological, being based over some pre-defined geographic region. Gaston and Matter (2002) proposed that the inclusion of more non-habitat, or area that is not used, in GIARs is one possible mechanism producing differences between PIARs and GIARs.

In this study, we examine the relationships between abundance, immigration and emigration and the landscape characteristics of site size and isolation. Additionally, we evaluate Gaston and Matter's (2002) hypothesis by comparing GIARs and PIARs for the same data. Specifically, we examine how density and the rates of immigration and emigration are related to both habitat area (GIAR) and host plant abundance (PIAR) for a monophagous butterfly *Parnassius smintheus* Doubleday (Lepidoptera: Papilionidae). We predict that because meadow area contains resources that are used by the butterflies and unusable area, butterfly density should decrease with increasing meadow area, but butterfly density should increase or remain constant with increasing host plant abundance. Monophages offer the opportunity to test assumptions concerning resources because their resource base is more easily defined.

METHODS

Study species and site.—Parnassius smintheus is abundant within alpine meadows in the Rocky Mountains, although related species are threatened elsewhere (Bas, 2002). The butterflies' larval host plant *Sedum lanceolatum* Torr. (Crassulaceae) is a perennial occurring in gravelly sites above tree-line (Fownes and Roland, 2002). *Parnassius smintheus* is univoltine with a flight period at our site from July to late August. Eggs are laid singly on low vegetation, on the ground, or occasionally on the host plant. Adult females tend to remain in areas with host plants present (Fownes and Roland, 2002) and males tend to aggregate where females are present (Matter and Roland, 2002). Males fly more frequently than females, which often search for oviposition sites by crawling. Despite these differences, estimated dispersal distances do not differ between the sexes (Roland *et al.*, 2000). Most dispersal occurs

TABLE 1.—Summary of meadow characteristics and *Parnassius smintheus* population data. Meadow C was not sampled in 1996. Four other meadows in the landscape were censused for butterflies, thus the number of immigrants does not equal emigrants. Because *Sedum* abundance was not collected in a similar manner in these meadows, they were excluded from analyses

				P. smintheus					
				Abundance		Immigrants		Emigrants	
Meadow	Connectivity	Area (ha)	*Sedum* abundance	1995	1996	1995	1996	1995	1996
C	9.53	4.1	4690	10.0	—	0	—	0	—
D	10.19	8.7	2939	38.0	120.7	5	1	2	2
d	9.19	1.1	356	1.2	0.0	2	2	1	0
E	3.32	9.2	20,080	58.3	124.0	2	2	6	3
F	5.28	3.0	16,801	31.6	65.5	3	1	1	5
G	9.94	8.5	40,081	60.0	84.1	9	17	11	14
g	10.18	2.5	5800	42.4	133.0	7	13	8	13
I	6.07	4.1	8693	1.0	65.0	0	0	0	0
J	9.30	26.2	40,154	3.0	58.7	1	4	2	3
L	5.51	18.5	39,210	9.0	116.0	3	5	2	4
M	4.43	25.6	18,276	26.5	230.0	2	2	3	2
N	3.54	1.3	4297	0.0	22.5	0	0	0	1
O	4.27	2.3	5330	4.3	13.3	1	3	0	3
P	4.64	7.7	3540	10.0	76.9	1	10	2	5
Q	6.84	10.2	5256	6.6	102.7	1	5	1	9
R	2.37	1.3	3264	6.9	36.0	0	0	0	0
Y	1.88	0.8	3986	5.8	0.0	2	0	1	0

through non-forested areas and there is little dispersal across valleys (Keyghobadi *et al.*, 1999; Roland *et al.*, 2000).

We conducted mark-recapture and host-plant mapping in 21 meadows located above tree-line (~2100 m) along Jumpingpound and Lusk ridges, Alberta, Canada (51°57′N, 114°54′W, *see* Keyghobadi *et al.*, 1999 for a map of the study area). The meadows are dominated by grasses, mountain avens and wildflowers including *Sedum lanceolatum.* Meadows are bordered on their lower slopes by forest consisting of *Picea engelmannii* Parry, *Pinus contorta* Loudon and *Abies lasiocarpa* (L.). We determined the geographical area of each meadow from black and white aerial photographs (1:20,000) taken in 1993 (Roland *et al.*, 2000). We used photographs with the meadows centered to minimize distortion due to photographic parallax. Meadow isolation was measured as connectivity, the inverse of isolation (Moilanen and Nieminen, 2002). Connectivity and related parameters were estimated using the methods of Hanski *et al.* (2000). As habitat type (forest or meadow) has been shown to affect dispersal (Roland *et al.*, 2000), distance composed of both habitats were included. All distances were measured from the centroids of butterfly capture in each meadow (Roland *et al.*, 2000).

Mark-recapture.—We sampled butterflies in each meadow three to four times over 5 wk periods in 1995 and 1996. We hand netted butterflies and each newly captured individual was given a unique 3 letter mark on the hind wings using a felt-tipped pen. For all captures we recorded the date, the butterfly's sex and identity mark and x, y coordinates from a grid overlaying the aerial photograph. The coordinates were accurate to ~20 m (Roland *et al.*, 2000). To ensure equal sampling effort among meadows, we recaptured until 75% of all butterflies caught had been previously captured that day.

We estimated butterfly population size in each meadow, on each sample date, using

TABLE 2.—Summary of tests of the relationships between connectivity and site size metrics and butterfly abundance and movement data. Connectivity was entered into each model and additional effects of site size were evaluated. An (*) indicates significance ($P < 0.05$). Note that deviance differs between models with the same dependent variable due to differences in weighting for dispersion

	Meadow area		*Sedum* abundance	
	1995	1996	1995	1996
Abundance				
Null deviance	15.45	28.17	18.71	18.03
Connectivity	0.52 ± 0.57	0.40 ± 0.41	0.52 ± 0.57	0.40 ± 0.41
χ^2	0.90	1.73	1.09	1.11
β	0.25 ± 0.27	0.53 ± 0.16	0.36 ± 0.22	0.29 ± 0.17
χ^2 $(\beta = 1)$	7.31*	8.25*	6.76*	15.85*
χ^2 $(\beta = 0)$	0.85	12.20*	3.02	4.38*
Immigration				
Null deviance	21.84	20.21	25.12	19.52
Connectivity	1.16 ± 0.55	1.51 ± 1.29	1.17 ± 0.52	1.51 ± 1.29
χ^2	5.55*	6.68*	6.38*	4.30*
β	0.04 ± 0.23	0.17 ± 0.26	0.22 ± 0.17	0.23 ± 0.20
χ^2 $(\beta = 1)$	16.30*	9.14*	16.60*	7.05*
χ^2 $(\beta = 0)$	0.03	0.46	1.79	0.93
Emigration				
Null deviance	14.59	23.72	20.85	23.05
Connectivity	0.86 ± 0.68	1.40 ± 0.47	0.86 ± 0.68	1.40 ± 0.47
χ^2	1.75	9.34*	2.42	9.07*
β	0.24 ± 0.31	−0.12 ± 0.22	0.43 ± 0.23	0.10 ± 0.19
χ^2 $(\beta = 1)$	5.40*	24.34*	4.85*	19.87*
χ^2 $(\beta = 0)$	0.59	0.29	3.98*	0.26

Craig's method (Craig, 1953; Roland *et al.*, 2000). Here, the number of captures in each sampling period is assumed to be Poisson distributed. The number of individuals never caught is estimated from the zero-term of the distribution and is added to the number of individuals captured to arrive at a population estimate. We calculated abundance in each meadow as the mean of the 3–4 estimates. Thus, our estimates should be considered as relative indices of population size rather than absolute estimates. We tallied the number of immigrants arriving at and emigrants leaving each meadow directly from the mark-recapture data. This method underestimates the total number of dispersing butterflies, but should be unbiased as sampling effort was equal in each meadow.

Host-plant abundance.—In 1995 we established continuous transects in 17 of the 21 meadows. Each transect was separated by 10 m and extended the length of each meadow. Within each 10 m long by 2 m wide segment of the transect, we counted all *Sedum lanceolatum* plants. A varying number of transects were used per meadow to allow proportional cover of each meadow. Positions of each segment were assigned *x, y* coordinates and "maps" of *S. lanceolatum* abundance were constructed. To arrive at an abundance of *Sedum* within each meadow, we multiplied mean *Sedum* density by the area over which *Sedum* occurred. The program CALHOME was used to calculate the area of *Sedum* occurrence as the minimum convex polygon over which there was at least one plant present.

Analyses.—We used generalized linear models with Poisson errors to examine relationships with area and compare PIARs and GIARs (Matter, 1997). Because isolation has been

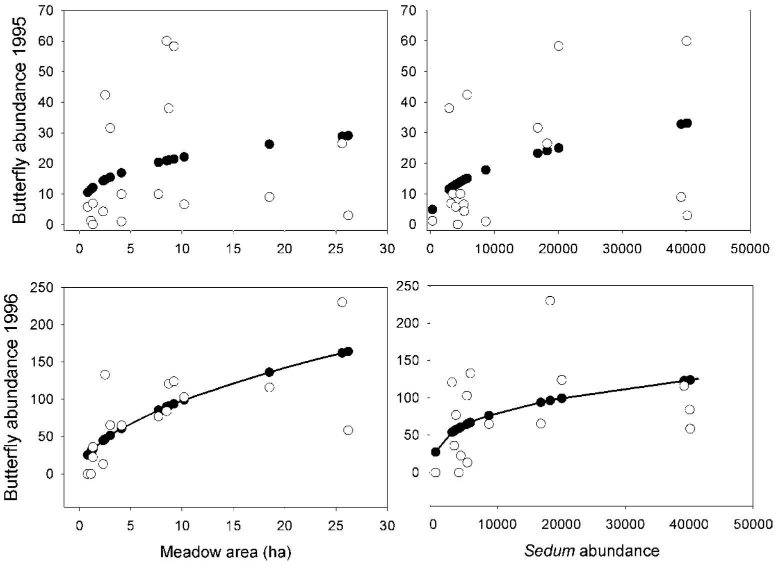


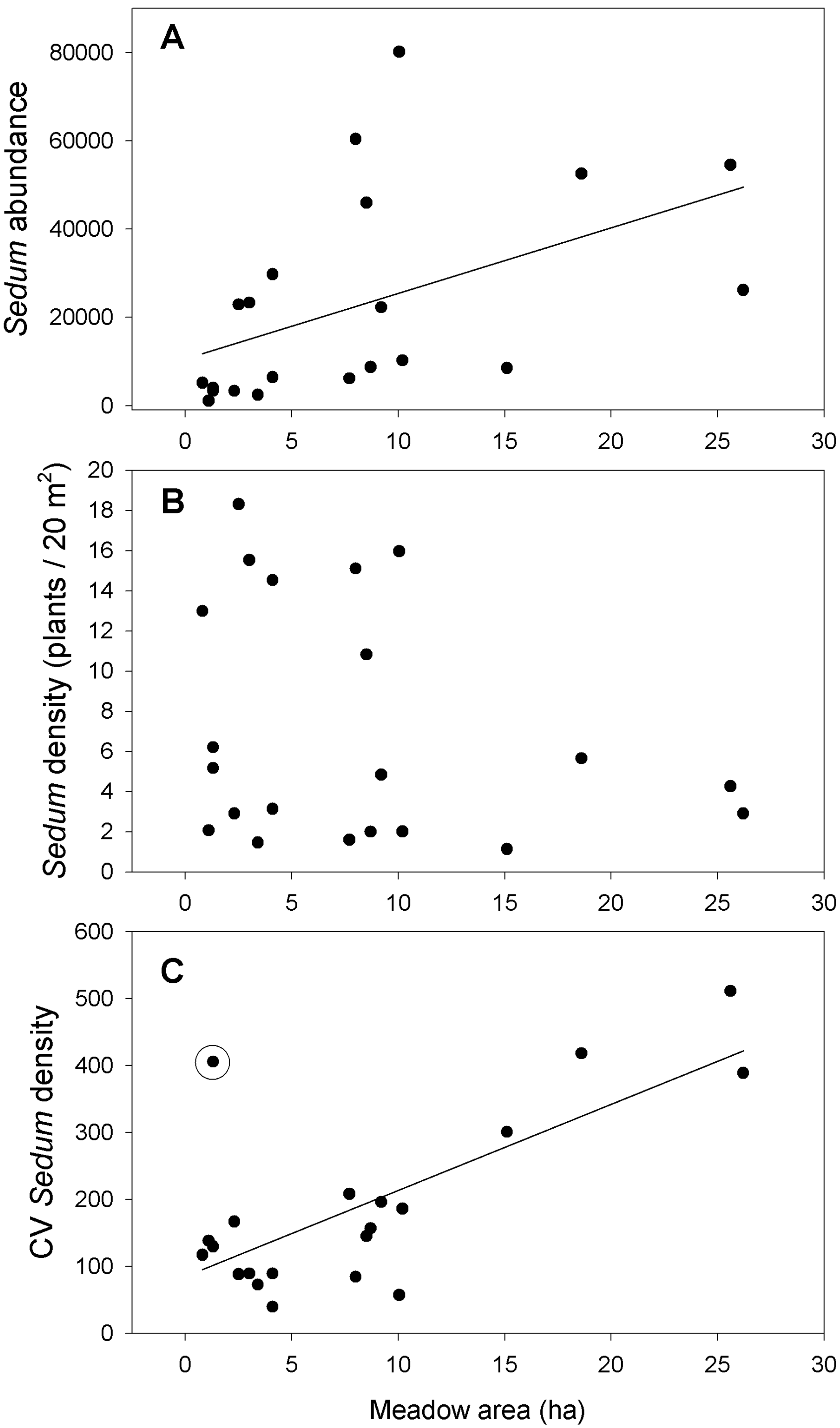
FIG. 1.—The relationships between *Paranassius smintheus* abundance and meadow area (left) and *Sedum* abundance (right). Open points represent data and closed points are fitted values. Significant fits for the test of $\beta = 0.0$ are shown with a line. Values and fits shown are not adjusted for the effects of connectivity nor overdispersion. For the sake of clarity, data is presented on a linear scale

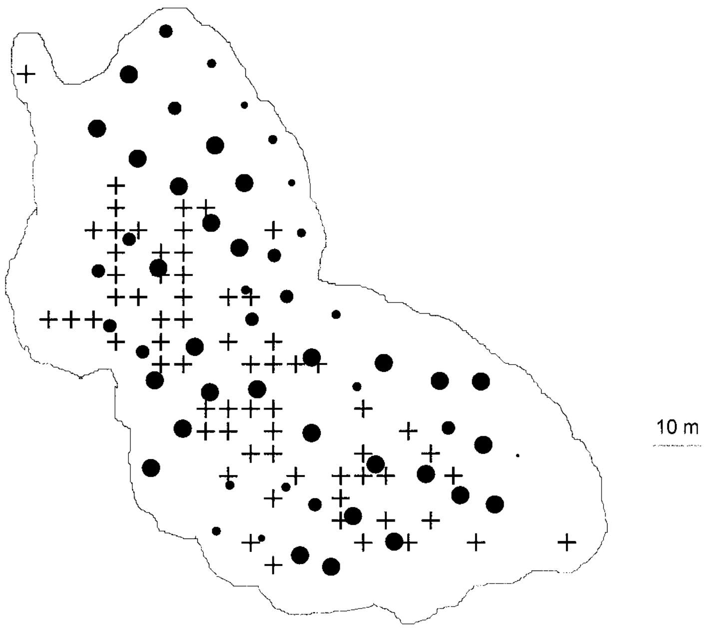
shown to be important for the dispersal of this species (Roland *et al.*, 2000), connectivity was entered into the model first and additional effects of site size were then analyzed. Separate models using either meadow area or *Sedum* abundance were fitted to butterfly abundance, immigration and emigration. We tested the slope (β) of each relationship versus hypotheses of $\beta = 0$ and $\beta = 1$. The test of $\beta = 0$ determines if there is a significant increasing or decreasing relationship with the independent variable (area or host plant abundance). The test of $\beta = 1$ determines if the *density* or *rate* of immigration or emigration varies with meadow area or host plant abundance. For example, a slope of one would indicate a constant density or rate of immigration or emigration with site size, whereas a slope >1 would indicate that the density of butterflies or the rate of immigration or emigration increases with site size.

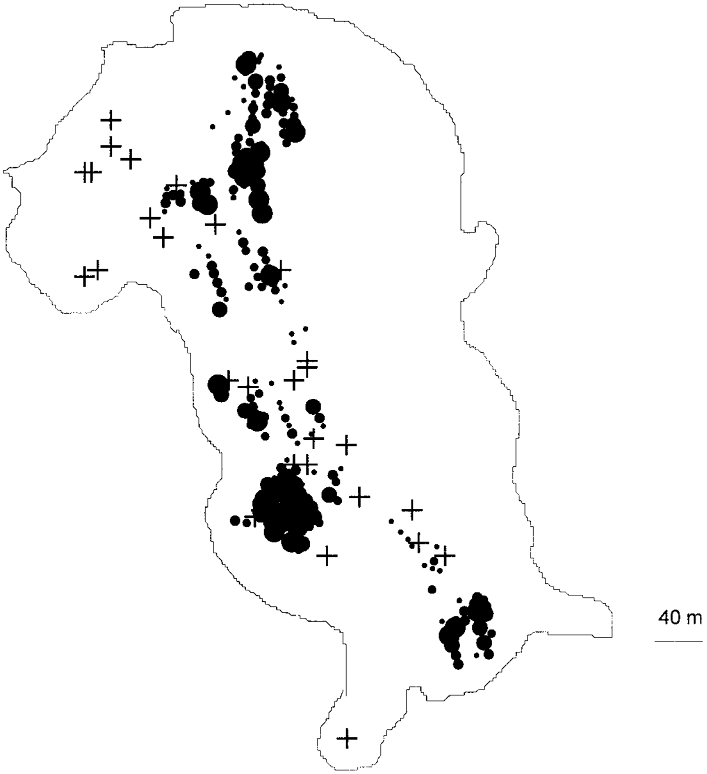
For each test, the deviance difference is approximately χ^2-distributed with one degree of freedom, which we used to determine significance. All data were overdispersed (*see* Connor *et al.*, 1997 for tests of overdispersion). Therefore, we jointly modeled the mean and

→

FIG. 2.—The relationships between *Sedum* abundance (A), *Sedum* density (B), and the coefficient of variation in *Sedum* density (C); and meadow area. *Sedum* abundance was positively related to meadow area ($F_{1,19} = 5.96$, $P = 0.03$, $R^2 = 0.24$). *Sedum* density showed no significant, linear relationship with meadow area ($F_{1,19} = 1.44$, $P = 0.24$, $R^2 = 0.07$), but the coefficient of variation (CV) in *Sedum* density increased with meadow area ($F_{1,19} = 20.45$, $P < 0.01$, $R^2 = 0.52$). The circled point in C indicates a statistical outlier. If this point is omitted, $F_{1,18} = 58.75$, $P < 0.01$, $R^2 = 0.87$, $cv = 14.9 \pm 1.9(\text{AREA}) + 52.4 \pm 21.9$.N.B., all 21 meadows were included in these analyses


A
Sedum abundance
80000
60000
40000
20000
0
0
5
10
15
20
25
30
B
Sedum density (plants / 20 m^2)
20
18
16
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30
C
CV *Sedum* density
600
500
400
300
200
100
0
0
5
10
15
20
25
30
Meadow area (ha)


10 m


40 m

dispersion by dividing each observation by the estimated dispersion (McCullagh and Nelder, 1989). The estimate of dispersion was derived from the full model, in which connectivity and either metric of site size was used. We used similar models for abundance, immigration and emigration; however, for emigration, we excluded from analyses meadows that had no butterflies in that year.

To investigate how resources vary with habitat area, we examined the relationships between meadow area and *Sedum* abundance, mean *Sedum* density and the coefficient of variation in *Sedum* density. For these tests, *Sedum* abundance was calculated over the entire meadow area. We calculated the coefficient of variation among all transect segments within each meadow to address how variable *Sedum* density is within meadows. A high coefficient of variation would indicate that a meadow contains a wide range of *Sedum* density. For each independent variable, we conducted a separate linear regression.

RESULTS

There were 1564 captures of 839 individuals in 1995 and 1200 captures of 757 individuals in 1996. There were 47 between meadow movements in 1995 and 68 in 1996 (Table 1). Four meadows were not analyzed due to a different method of host plant data collection. Meadows ranged in size from 0.8 to 26.3 ha and the abundance of *Sedum lanceolatum* ranged from 356 to 40,154 plants per meadow. Connectivity ranged from 1.88 (most isolated) to 10.19.

Butterfly abundance in either year was not significantly related to meadow connectivity (Table 2). The number of immigrating butterflies increased with meadow connectivity in both years, and the number of emigrating butterflies increased with connectivity in 1996. After accounting for the effects of connectivity, the abundance of *Parnassius smintheus* (test of $\beta = 0$) increased with meadow area and with *Sedum* abundance in 1996 (Fig. 1), but showed no relationship to either metric of site size in 1995. The number of immigrating butterflies was not related to meadow area or *Sedum* abundance either year. The number of emigrants increased with increasing *Sedum* abundance in 1995, but showed no other significant relationships.

The density of butterflies (test of $\beta = 1$) decreased with increasing meadow area in both years (Fig. 1, Table 2). The density of *Parnassius smintheus* also decreased with increasing *Sedum* abundance in both years. The rate of immigration decreased with increasing meadow area and with *Sedum* abundance in both years. Similarly, the rate of emigration decreased with increasing meadow area and *Sedum* abundance in both years.

Sedum abundance increased with increasing meadow area (Fig. 2), whereas the mean density of *Sedum* showed no statistical, linear relationship to meadow area. The coefficient of variation in *Sedum* density increased with increasing meadow area.

DISCUSSION

Although there were 3 of a possible 12 statistically significant relationships, neither meadow area nor *Sedum* abundance explained a large proportion of deviance in the

---

←

FIG. 3.—The distribution of *Sedum* density (circles) and butterfly captures (crosses) in two meadows. The size of the circles is proportional to *Sedum* density and there is no circle where *Sedum* density is zero. The meadow on top (g) is 2.5 ha and the other (J) is 26.2 ha. Note that the scale is not the same for each meadow

abundance, immigration and emigration of *Parnassius smintheus* (<1 to 43% of null deviance). In general, *Sedum* abundance explained more deviance in butterfly movement and abundance than did meadow area, although this was not universally true. This result is comparable to that of Brommer and Fred (1999), who found in a study of *P. apollo* L., that the proportion of observations of butterflies was positively related to the area covered by its host plant, *S. telephium* L., but was not related to outcrop (habitat) area. The lack of consistently strong relationships with either meadow area or *Sedum* abundance for *P. smintheus* is surprising given theory (Hanski, 1999) and the number of studies showing such relationships (Bowers and Matter, 1997; Connor *et al.*, 2000). That abundance and movement vary with site area should not be taken for granted. In a study examining the abundance of vertebrates in fragments of Florida scrub habitat, McCoy and Mushinsky (1999) found that the abundance of only 61% of the species increased with scrub area. In our study, it was somewhat reassuring that the trends were usually in expected directions, albeit with much variation.

The immigration of butterflies in both years, and emigration in one year, was related to meadow connectivity, but the abundance of butterflies was not. Isolation has been shown to influence the immigration of a variety of species (*see* Moilanen and Nieminen, 2002); effects of isolation on emigration are rarer. Theory provides little guidance on how isolation may affect emigration. Our results are somewhat equivocal, showing that the number of emigrants increased with connectivity in 1996, but there was only an insignificant trend in 1995. Decreasing 'emigration' with isolation may be an artifact of the mark-recapture methodology in that we can only observe successful emigrants, *i.e.*, those that arrive in another meadow. Alternatively, we may expect more successful emigration from meadows that are less isolated (Hanski *et al.*, 2000). The lack of an effect of connectivity on butterfly abundance indicates that immigration may be only a small component of population size. This result is also reflected in the mark-recapture data showing few migration events. Similarly low rates of dispersal have been inferred from genetic data (Keyghobadi *et al.*, 1999).

Many factors not considered here likely affect local population size and dispersal. In an analysis of the number of dispersal events between pairs of meadows, Roland *et al.* (2000) found that movement increased with the number of butterflies marked in the source meadow and the population size in the target meadow; the number of movements decreased with increasing isolation, elevation change and population size in the source meadow. Subsequently, Matter and Roland (2002) showed that some of this conspecific attraction, where immigration is greater to large populations and there is low emigration from large populations, is related to mating opportunity. In an experimental setting, the immigration and abundance of male *Parnassius smintheus* was positively related to female abundance, but emigration was not (Matter and Roland, 2002). Additionally, they found that increasing abundance of nectar flowers increases immigration but does not affect emigration (Matter and Roland, 2002). Part of the reason habitat area is a poor predictor of immigration for *P. smintheus* may lie in the linear configuration of meadows. Most meadows tend to be aligned end to end along ridges. In general, *P. smintheus* do not move as easily through forested habitat as they do through meadow or open habitats (Roland *et al.*, 2000). Thus, encountering a meadow for a dispersing butterfly may be based more on the amount of open boundary between meadows than on meadow area. The lack of effect of area on immigration seen here is in agreement with Roland *et al.* (2000) who found no effect of meadow area on movement between meadow pairs.

Despite the weak relationships, the model parameters offer the best estimate of the relationships of population size with site size. As predicted by Gaston and Matter (2002), the density of butterflies decreased with increasing meadow area (GIAR). Although the relationship between *Sedum* density and meadow area was not significant (Fig. 2B), it does show a distinct pattern. Large meadows tend to have low densities of *Sedum,* whereas small meadows are of two types, either high or low *Sedum* density. This trend is better reflected in the coefficient of variation in *Sedum* density. In large meadows, there are often areas of high *Sedum* density interspersed by grassy areas with little or no *Sedum* (Fig. 3). Similarly, small meadows have either uniformly high or uniformly low *Sedum* density, except for one meadow that is patchy in its distribution of *Sedum,* the outlier in Figure 2C. These observations are in accord with the biology of *Sedum* which tends to grow most abundantly on steep, well-drained, gravelly slopes, primarily 20–40 m above tree-line. Large meadows tend to contain both gravelly slopes and grassy areas with little *Sedum.* Small meadows are of one type or the other. Thus, increasing amount of non-habitat affects the GIAR for *Parnassius smintheus,* but only in the transition from small high *Sedum* density meadows to large meadows. However, it does not appear that decreasing butterfly density with increasing meadow area (the GIAR) is due solely to an increasing amount of non-habitat in larger meadows. In addition, the pattern arises from decreasing butterfly density with increasing host plant abundance. That is, the underlying PIAR shows a negative relationship. Thus, there may be multiple mechanisms responsible for decreasing generalized individuals area relationships.

Acknowledgments.—Mark recapture and plant mapping were assisted by N. Ambrose, M. Caldwell, S. Cotterill, M. Forrester, F. Johnson, C. Schmidt, L. Scott, K. Ward and A. Winship. We thank J. Brommer, E. Connor, T. Culley, E. McCoy and two anonymous reviewers for their comments. Research was supported by grants from NSF (DEB-0212776), Friends of Banff National Park, Alberta Sports Recreation Parks and Wildlife Foundation, Banff National Park and NSERC, Canada.

LITERATURE CITED

BAS, N. 2002. Nectar plant sources for the threatened Apollo butterfly (*Parnassius apollo* L. 1758) in populations of central Spain. *Biological Conservation,* **103**:277–282.

BENDER, D. J., T. A. CONTERAS AND L. FAHRIG. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology,* **79**:517–533.

BOWERS, M. A. AND S. F. MATTER. 1997. Landscape ecology of mammals: relationships between density and patch size. *J. Mammal.,* **78**:999–1013.

BROMMER, J. E. AND M. S. FRED. 1999. Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. *Ecol. Entomol.,* **24**:125–131.

CONNOR, E. F., A. C. COURTNEY AND J. M. YODER. 2000. Individuals-area relationships: the relationship between animal population density and area. *Ecology,* **81**:734–748.

———, E. H. HOSFIELD, D. A. MEETER AND X. NIU. 1997. Tests for aggregation and size-based sample-unit selection when sample units vary in size. *Ecology,* **78**:1238–1249.

——— AND E. D. MCCOY. 1979. The statistics and biology of the species-area relationship. *Am. Nat.,* **113**:791–833.

CRAIG, C. C. 1953. On the utilization of marked specimens in estimating populations of flying insects. *Biometrika,* **40**:170–176.

ELTON, C. 1933. The ecology of animals. Methuen, London, United Kingdom. 97 p.

FOWNES, S. AND J. ROLAND. 2002. Effects of meadow suitability on female behaviour in the alpine butterfly, *Parnassius smintheus* Doubleday. *Ecol. Entomol.,* **27**:457–466.

GASTON, K. J., T. M. BLACKBURN AND R. D. GREGORY. 1999. Does variation in census area confound density comparisons? *J. Appl. Ecol.,* **36**:191–204.

——— AND ———. 2000. Pattern and process in macroecology. Blackwell, Oxford, United Kingdom. 377 p.

——— AND S. F. MATTER. 2002. Individuals-area relationships: comment. *Ecology,* **83**:288–293.

HAILA, Y. 1988. Calculating and miscalculating density: the role of habitat geometry. *Ornis Scandinavica,* **19**:88–92.

HANSKI, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, United Kingdom. 313 p.

———, J. ALHO AND A. MOILANEN. 2000. Estimating the parameters of survival and migration in metapopulations. *Ecology,* **81**:239–251.

KEYGHOBADI, N., J. ROLAND AND C. STROBECK. 1999. Influence of landscape on the population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). *Mol. Ecol.,* **8**:1481–1495.

LOMOLINO, M. V. 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos,* **57**:297–300.

MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, U.S.A. 203 p.

MATTER, S. F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. *Oecologia,* **105**:447–453.

———. 1997. Population density and area: the role of between- and within-patch processes. *Oecologia,* **110**:533–538.

———. 1999. Population density and area: the role of within- and between generation processes over time. *Ecol. Model.,* **118**:261–275.

———. 2000. The importance of the relationship between population density and habitat area. *Oikos,* **89**:613–619.

———. 2001. Synchrony, extinction, and dynamics of spatially segregated heterogeneous populations. *Ecol. Model.,* **141**:217–226.

——— AND J. ROLAND. 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of *Parnassius smintheus. Ecol. Entomol.,* **27**:308–316.

MCCULLAGH, P. AND J. F. NELDER. 1989. Generalized linear models, 2nd ed. Chapman and Hall, New York, New York, U.S.A. 511 p.

MOILANEN, A. AND M. NIEMINEN. 2002. Simple connectivity measures in spatial ecology. *Ecology,* **83**:1131–1145.

ROLAND, J., N. KEYGHOBADI AND S. FOWNES. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology,* **81**:1642–1653.

ROOT, R. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea. Ecol. Monog.,* **43**:95–194.

SCHOENER, T. W. 1986. Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist?, p. 556–586. *In:* J. Diamond and T. J. Case (eds.). Community ecology. Harper and Row, New York, New York, U.S.A. 665 p.

SIMBERLOFF, D. 1976. Experimental zoogeography of islands: effects of island size. *Ecology,* **57**:629–648.

SMALLWOOD, K. S. AND C. SCHONEWALD. 1996. Scaling population density and spatial pattern for terrestrial, mammalian carnivores. *Oecologia,* **105**:329–335.

SUBMITTED 4 NOVEMBER 2002 ACCEPTED 3 MARCH 2003