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MIGRATION AND SURVIVAL OF *PARNASSIUS SMINTHEUS*: DETECTING EFFECTS OF HABITAT FOR INDIVIDUAL BUTTERFLIES

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Abstract. We examined the migration and survival of the butterfly *Parnassius smintheus* in a heterogeneous landscape consisting of 21 habitat patches imbedded in a matrix of meadow and forest habitat. We modified an existing mark–release–recapture model to account for multiple habitat types and fit the model to data for 839 and 873 individuals in two separate years. Migration was infrequent with only 24 and 27 observed movements between patches in each year. Daily within-patch survival was moderate ($>$0.90) and did not vary greatly with patch isolation. Estimated mortality during migration was low, but increased markedly for isolated populations. Despite the limited data, the model showed that forest matrix habitat reduced migration distance to a greater degree than did meadow habitat, indicating that the effective isolation of populations depends on both the habitat type and the distance between populations. This result concurs with previous investigations of these data, demonstrating the utility of the model even when movement is infrequent. Studies of migration are often hampered by few observable events. Our model provides reasonable estimates given few migration events. The ecological results of this study illustrate the need for spatial population studies to account for the effects of different habitat types on the migration of individuals among habitat patches. Our results also suggest management options for the conservation of endangered *Parnassius* species in other parts of the world.

Key words: butterflies; connectivity; dispersal; habitat patch; mark–recapture; metapopulation; mortality; Parnassius smintheus.

INTRODUCTION

Understanding and predicting the migration of individuals is an important aspect of ecology as well as conservation and remediation plans. Migration affects local population dynamics and gene flow, and can produce emergent properties for groups of local populations. Often, due to fragmentation and habitat loss, species that are at risk exist in isolated habitat patches surrounded by non-habitat patches. In these situations, the migration of individuals may be highly important for population dynamics and persistence. In general, physical factors such as the distance between populations and the size of habitat patches have been used to predict migration among populations (Hanski 1994, Matter 1996, 1997); however, other factors have been neglected (Wiens 1997, Tischendorf and Fahrig 2000, Crone et al. 2001). One important factor that may affect migration is the type of habitat through which organisms move (Pither and Taylor 1998, Haddad 1999, Ricketts 2001). An effect of habitat type on migration is implicit in the literature concerning boundary effects; for instance, the contrast between ‘‘soft’’ and ‘‘hard’’ edges (Stamps et al. 1987, Moilanen and Hanski 1998). Organisms using and moving through habitats differently provide the theoretical basis for habitat corridors (Simberloff et al. 1992) and part of the reasoning for protective hedgerows around crops (Racette et al. 1992). Although the habitat immediately surrounding patches has been shown to affect migration (Kuussaari et al. 1996), the effects of habitat type on migration in general are just beginning to be investigated (Pither and Taylor 1998, Bowne et al. 1999, Haddad 1999, Roland et al. 2000, Ricketts 2001). Differences in the ability of organisms to move through different habitat types may alter predictions of population persistence and dynamics (i.e., estimates derived in one system may not apply to others if habitats differ). Similarly, multiple habitats within a system may alter predictions if there are differences in migration through them.

Here, we investigate the migration of the Rocky Mountain Apollo butterfly, *Parnassius smintheus*, in a network of 21 habitat patches and demonstrate a simple method to quantify the effects of different habitat types on migration using relatively few data. Providing comparison, Roland et al. (2000) used this data to examine the effects of habitat type on migration between pairs of patches and found that intervening forest decreased

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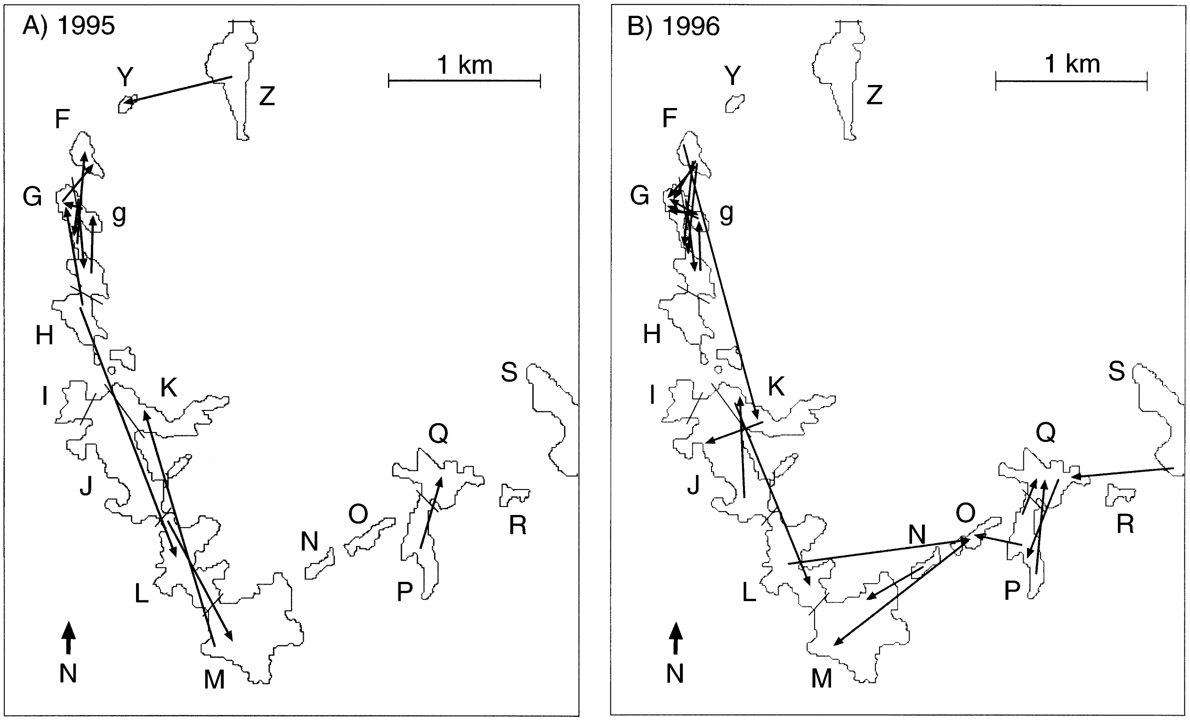

FIG. 1. Meadows along Jumpingpound Ridge (Alberta, Canada) and between meadow movements of *Parnassius smintheus*. Panel A shows movements in 1995; panel B shows movements in 1996. Enclosed areas are meadow habitat; other areas are forested. In some cases, the delineation between meadows was an arbitrary boundary indicated by a solid straight line. Each movement is shown with an arrow. The tail and head indicate position of capture and recapture, respectively. Note that arrows depict straight-line movement while the model assumes that dispersal is occurring along the ridgetop from and to centroids of butterfly capture in each meadow. Four meadows (C, D, d, and E) on Lusk Ridge, 4 km to the northwest, are not shown. All migration events for these meadows were contained within Lusk Ridge. For a complete depiction of the study area, see Keyghobadi et al. (1999).

the number of migrants to a greater degree than did open meadow habitat. We extend the virtual migration (VM) model, a multi-strata, mark–recapture model developed by Hanski et al. (2000), to account for migration through different habitat types. This modification offers the opportunity to compare the effects of habitat types on movement at the level of individual butterflies, rather than bulk movement for local populations. In addition, the model provides comparable estimates of patch-based rates of dispersal and mortality, and, importantly, estimates of mortality occurring during migration. We also assess the importance of habitat patch size and quality on the survival and migration of butterflies, and directly compare the influence of habitat type with the effects of the spatial geometry of the focal habitat.

METHODS

Natural history

Parnassius smintheus Doubleday (Lepidoptera: Papilionidae) is a medium-sized butterfly with a mean wingspan of ~5.5 cm. The species is sexually dimorphic with males having a white to yellowish ground color and females a darker, translucent appearance. Both sexes have dark spots on the forewings, a dark marginal band, and from none to several red spots on the hind and forewings. *Parnassius smintheus* is abundant within subalpine meadows in the Rocky Mountains from New Mexico to the Yukon, although congeners are threatened elsewhere (Heath 1981). Across their range, *P. smintheus* feed on several stonecrop (*Sedum*) species (Guppy and Shepard 2001). At our site, the larval host plant is lance-leaved stonecrop, *Sedum lanceolatum* Torr., which occurs predominantly in gravelly sites above tree line (Fownes and Roland 2002). *Parnassius smintheus* is univoltine with a flight period from mid-July to September in our study area. Adult males are generally more apparent than the sedentary females. Nonetheless, estimated dispersal distances are equal between the sexes (Roland et al. 2000). Butterflies feed on nectar from species such as *Sedum lanceolatum*, *Solidago multiradiata* (alpine goldenrod), and *Senecio lugens* (black-tipped groundsel; see Matter and Roland 2002).

Study area

Mark–recapture of *P. smintheus* was conducted in a network of 21 meadows (Fig. 1) located above tree line

TABLE 1. Parameters, their definitions, and units used in the virtual migration model.

Symbol	Parameter	Type	Units
ϕ_p	Within-patch survival	fitted parameter	1/time (d)
ε_j	Probability of emigration	calculated	1/time
A_j	Emigration from patch of unit area	fitted parameter	
η	Patch area relative to unit area	data	(ha, *Sedum* plants)
ζ_{em}	Scaling of emigration with patch area	fitted parameter	
ϕ_{mj}	Probability of surviving migration	calculated	1/event
S_j	Connectivity	calculated	
$d_{j,k}$	Distance between patches j and k	data	d (km)
α	Inverse of mean migration distance	fitted parameter	$1/d$
ζ_{im}	Scaling of immigration with patch area	fitted parameter	
λ	Migration mortality shape constant	fitted parameter	
$\psi_{j,k}$	Probability of migration between patch j and k	calculated	1/time

Notes: Parameters subscripted with a j are patch specific, and probabilities apply to individuals. The specific units in parentheses were used in this study.

(~2100 m) along Jumpingpound Ridge, Alberta, Canada (51°57′ N, 114°54′ W). Each meadow was considered a ''habitat patch.'' This distinction is largely based on human perception, with each meadow containing host and nectar plants as well as *P. smintheus*, although not all area within each meadow is suitable habitat (Matter et al. 2003). The delineation between meadows in some cases was an arbitrary distinction between contiguous parts of large meadows (lines between meadows, Fig. 1). 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 Engelmann spruce (*Picea engelmannii*). The area (ha) of each meadow was estimated from aerial photographs (1:20 000) taken in 1993 (Roland et al. 2000). We used photographs with meadows centered to minimize distortion due to photographic parallax. We allowed the butterflies to define the location of patches. The distance (km) between patches comprised of forest and meadow habitat was estimated based on the centroids of butterfly captures within each meadow. Interpatch distances were measured along ridgetops, as butterflies tend to follow ridges when dispersing, and genetic evidence (Keyghobadi et al. 1999) and mark–recapture evidence (Roland et al. 2000) suggest that there is little dispersal across valleys.

Mark–recapture and host plant abundance

Butterflies were censused three to four times in each patch over a 5-wk period in 1995 and 1996. We captured butterflies using hand nets and each was given a unique 3-letter mark on the hind wing. For all captures, we recorded the date, location based on *x, y* coordinates, sex, and identity mark. Location was accurate to ~20 m (Roland et al. 2000). To equilibrate effort among meadows, capture continued until ~75% of butterflies had been recaptured that day.

We quantified *S. lanceolatum* abundance for most meadows in 1995 with additional censusing in 1998. *Sedum* changes little in abundance and distribution over such a time interval (Fownes 1999). We established transects, separated by 10 m, in each meadow and counted all plants within 2-m wide by 10-m long, nonoverlapping segments along the entire length of each transect. Transect lengths varied among meadows and a varying number of transects were used per meadow to ensure proportional coverage of each meadow. To arrive at an abundance of *Sedum* within each meadow, we multiplied mean *Sedum* density by meadow area. Note that the methods used here to calculate *Sedum* abundance differ from Matter et al. (2003).

The model

The virtual migration (VM) model is a mark–recapture model using biological assumptions to estimate the survival within and migration among populations (Hanski et al. 2000). The biological basis and statistical fitting of the model have been described elsewhere (Hanski et al. 2000). The model is based on discrete events, in our case occurring daily. First, an individual survives in a patch with probability ϕ_p (Table 1). If the individual survives, it may either stay in that patch or emigrate. We model the probability of emigration as a function of patch area. Although the total number of emigrants from a population may increase with increasing population size (and thus habitat area), the probability of a given individual emigrating likely decreases in a nonlinear manner with patch area (Turchin 1986). Thus, the probability of an individual emigrating (ε) from patch j is related to its area (A_j,) by the power function

$$\varepsilon_j = \eta A_j^{-\zeta_{em}} \tag{1}$$

where $\eta > 0$ and $\zeta_{em} > 0$ describe emigration from a patch relative to unit size (1 ha or 10 000 *Sedum* plants) and the scaling of emigration with patch area, respectively. Emigrants survive migration with a patch-specific probability ϕ_{mj}, based on patch size and connectivity and immigrate within the same time interval. Connectivity can be thought of as the inverse of isolation where the contribution to a population's immigrant pool is determined by the distance weighted number of emigrants produced by all other populations

(Moilanen and Nieminen 2002). In the VM model, the situation is somewhat reversed in that we use connectivity from the perspective of an emigrant moving to a new population. The connectivity S_j, of patch j, is a function of the distance ($d_{j,k}$, in km) between patch j and k, the area of patch k, and how immigration scales with habitat area (ζ_{im}):

$$S_j = \sum_{k \neq j} \exp(-\alpha d_{j,k}) A_k^{\zeta_{\mathrm{im}}}. \tag{2}$$

The parameter α describes the effect of distance on migration. Mathematically, this parameter is the inverse of the mean migration distance (Hanski 1999). The probability of surviving migration ($\phi_{\mathrm{m}j}$) from patch j is a sigmoidally increasing function of the connectivity (S) of patch j and the parameter $\lambda > 0$, which alters the shape of the curve:

$$\varphi_{\mathrm{m}\,j} = \frac{S_j^2}{\lambda + S_j^2}. \tag{3}$$

The square root of λ defines the connectivity for which the probability of surviving migration is 0.5. Individuals that survive emigration from patch j are allotted to new patches according to the relative contribution of each patch to the connectivity of patch j. We may expect that patches that are large and close to the patch of emigration will receive a greater fraction of the immigrants than smaller, more distant patches (MacArthur and Wilson 1967). Thus, the probability of migrating from patch j to patch $k(\psi_{j,k})$ is

$$\psi_{j,k} = \frac{\exp(-\alpha d_{j,k}) A_k^{\zeta_{\mathrm{im}}}}{\dfrac{\lambda}{S_j} + S_j}. \tag{4}$$

Overall, the probability of migrating between patch j and k is based on (1) surviving in patch j, (2) emigrating from patch j (Eq. 1), (3) surviving emigration (Eq. 3), and (4) the distance between patch j and k and size of patch k, relative to the size and distance from other patches surrounding j (Eq. 4).

The primary difference between our model and that described by Hanski et al. (2000) is in the calculation of connectivity. In our model, the connectivity S_j, of patch j, is a function of the distance between patch j and patch k comprising two habitat types, forest ($d_{\mathrm{f}j,k}$) and meadow ($d_{\mathrm{m}j,k}$), each with its respective parameter (α_{f} and α_{m}) describing the effect of that habitat type on migration distance:

$$S_j = \sum_{k \neq j} \exp(-\alpha_{\mathrm{f}} d_{\mathrm{f}\,j,k} - \alpha_{\mathrm{m}} d_{\mathrm{m}\,j,k}) A_k^{\zeta_{\mathrm{im}}}. \tag{5}$$

Because α describes the inverse of mean migration distance, we would expect greater migration distances through meadow than through forest habitat, and thus α_{f} to be greater than α_{m}, based on the findings of Roland et al. (2000).

The parameters ϕ_{p}, η, ζ_{em}, ζ_{im}, α_{f}, α_{m}, and λ, and daily capture probabilities are estimated using maximum likelihood. The data consist of individual capture histories for all butterflies. Using the functional forms and parameter values, each individual capture history is assigned a probability. The likelihood of the complete data is simply the product of the individual probabilities. Capture probabilities are assumed not to vary among patches within sampling periods. The values of $\phi_{\mathrm{m}j}$ and $\psi_{j,k}$ are not estimated independently, but can be calculated from the estimated model parameters. Parameter estimation was conducted using 1000 randomizations in simulated annealing (Moilanen 1995), followed by 10 000 intelligent randomizations to converge on the optimum (Hanski et al. 2000). Confidence intervals for the parameters were estimated based on likelihood ratio tests. Here, we used only 1000 evaluations, as one parameter is fixed and starting values are known. Replicate runs were conducted to check for convergence of parameter estimates and confidence intervals. Hanski et al. (2000) developed a statistic, $Q_i(t)$ to assess model lack of fit. This statistic evaluates how well the model describes individuals captured at time t in patch i that were captured at time $t - 1$, and is based on the familiar equation $(n_i - e_i)^2/v_i$, where n is the observed number, e is the expected number, and v is the variance. We aggregated this statistic across time periods to assess model fit for each patch. Examining model fit on a per patch basis, rather than for the model overall, allows for added biological interpretation (Wahlberg et al. 2002). Fits were assessed assuming a χ^2 distribution with degrees of freedom equal to the number of summands (Hanski et al. 2000).

We ran the VM model using both *Sedum* abundance and meadow area as a measure of meadow size. This approach allowed us to examine differences in migration that may be related to resources rather than to patch geometry.

RESULTS

There were 1136 captures of 839 individuals in 1995 and 873 captures of 759 individuals in 1996. The total number of observed movements between meadows was low, with 24 dispersal events in 1995 and 27 in 1996 (Table 2). The data here differ from Roland et al. (2000). In the present study, multiple captures and migration of an individual on the same date are excluded to meet the assumptions of the virtual migration (VM) model.

Parameter estimation

Estimates are based on relatively few migration events, resulting in wide confidence intervals for some parameters (Table 3). Despite these limitations, an effect of habitat type on migration is evident from the respective parameter estimates for meadow (α_{m}) and forest (α_{f}). The parameter estimates for forest habitat were significantly greater than for meadow habitat in 1995, indicating that forest habitat isolates populations to a greater degree than does meadow habitat (Fig. 2).

TABLE 2. Summary of meadow size and *Parnassius smintheus* data.

Meadow	Connectivity	Area (ha)	*Sedum* abundance	*P. smintheus*					
				Abundance		Immigrants		Emigrants	
				1995	1996	1995	1996	1995	1996
C	6.96	4.1	6417	10.0	···	0	···	0	···
D	7.73	8.7	8700	38.0	120.7	5	1	2	2
d	7.37	1.1	1133	1.2	0.0	2	2	1	0
E	2.85	9.2	22264	58.3	124.0	2	2	6	3
F	6.39	3.0	23295	31.6	65.5	3	1	1	5
G	8.51	8.5	45985	60.0	84.1	9	17	11	14
g	8.12	2.5	22887	42.4	133.0	7	13	8	13
H	4.41	3.4	2482	4.0	1.0	0	0	2	0
I	4.85	4.1	29766	1.0	65.0	0	0	0	0
J	7.57	26.2	38121	3.0	58.7	1	4	2	3
K	7.17	8.0	60400	18.3	40.1	1	2	0	2
L	4.07	18.5	52545	9.0	116.0	3	5	2	4
M	3.81	25.6	54528	26.5	230.0	2	2	3	2
N	5.53	1.3	3361	0.0	22.5	0	0	0	1
O	5.56	2.3	3335	4.3	13.3	1	3	0	3
P	4.64	7.7	6160	10.0	76.9	1	10	2	5
Q	6.88	10.2	10251	6.6	102.7	1	5	1	9
S	4.07	15.1	4030	1.0	13.6	0	0	0	1
R	2.01	1.3	8532	6.9	36.0	0	0	0	0
Y	3.47	0.8	5192	5.8	0.0	2	0	1	0
Z	1.26	10.1	80199	58.5	121.3	1	0	0	0

Notes: Butterfly abundance here was estimated using Craig's method (Craig 1953). Meadow C was not sampled in 1996. Mark–recapture was conducted over 39 days in 1995 and 43 days in 1996. In 1995, there were 24 movements between 14 different pairs of meadows (of 420 possible pairs), while in 1996 there were 27 movements between 18 different pairs. Note that the population data and *Sedum* abundance differ from those in Roland et al. (2000) and Matter et al. (2003). In the present study, migration occurring within a census period was excluded, and *Sedum* abundance was calculated over entire meadows. Connectivity was calculated using meadow area (ha), $\alpha_f = 3.13$/km, $\alpha_m = 2.31$/km, and $\eta = 0.23$.

In 1996, using *Sedum* abundance, the estimate for the effect of forest habitat on migration distance was significantly greater than the estimate for meadow habitat. However, the parameter estimate for meadow habitat was not significantly less than that for forest habitat (note that the point estimate for α_f falls inside the 95% confidence interval for α_m). Using meadow area as a metric of site size, there was no significant difference between forest and meadow in 1996, although the effect of forest was consistently greater. Using $1/\alpha$ as mean migration range (Hanski 1999), forest habitat decreases this distance by a factor of $\sim$2.9 compared to an equal amount of meadow habitat (i.e., somewhat greater than the value of 1.9 reported by Roland et al. [2000]). Daily within-patch survival (ϕ_p) was moderate, with $>90\%$ of the population surviving. Estimated survival was

TABLE 3. Parameter estimates from the virtual migration (VM) model (95% confidence intervals in parentheses) for *Parnassius smintheus* within 21 meadows at Jumpingpound Ridge, Alberta, Canada.

Parameter (units)	Meadow area		*Sedum* abundance†	
	1995	1996	1995	1996
α_f (1/km)	5.81 (2.78–10.39)	3.13 (1.36–7.92)	7.63 (4.29–12.98)	3.67 (1.69–7.91)
α_m (1/km)	1.34 (0.25–4.48)	2.31 (0.72–3.68)	2.36 (0.66–4.48)	2.16 (0.68–3.65)
ϕ_p (1/d)	0.91 (0.89–0.91)	>0.99 (0.99–1.00)	0.90 (0.89–0.92)	>0.99 (0.99–1.00)
λ‡	0.03 (0.00–0.20)	<0.01 (0.00–0.11)	0.04 (0.00–0.33)	0.27 (0.00–0.74)
η	0.04 (0.00–0.09)	0.01§	0.03 (0.02–0.04)	0.05 (0.03–0.08)
ζ_{em}	<0.01 (0.00–0.34)	0.23 (0.00–0.61)	0.13 (0.00–0.57)	0.41 (0.00–0.83)
ζ_{im}	0.39 (0.13–3.00)	0.79 (0.00–1.23)	1.93 (0.73–3.99)	1.06 (0.34–1.86)

Notes: Estimates are shown for models using either meadow area or host plant abundance (*Sedum lanceolatum*) as a metric of site size. Parameter estimates for *Sedum* are based on 10 000 plants, rather than 1 ha.

† To arrive at an abundance of *Sedum* within each meadow, we multiplied mean *Sedum* density by meadow area.

‡ Lambda from models using meadow area cannot be directly compared to those using *Sedum* abundance as they are based on different units.

§ The model did not converge for this estimate.

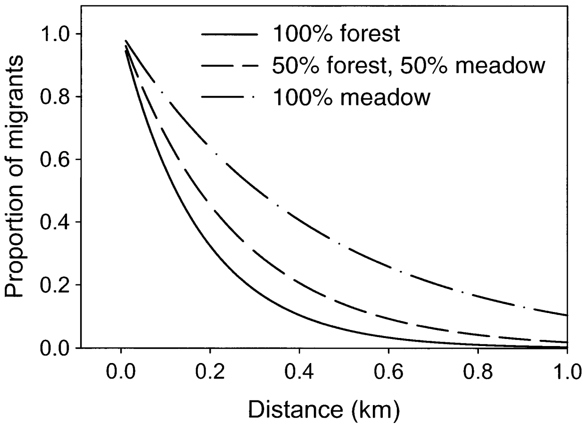

FIG. 2. The effects of habitat type on the migration of *P. smintheus*. Dispersal distances up to 1 km are shown. Values of 5.65/km and 2.26/km (mean alphas for 1995 and 1996 estimated using *Sedum* abundance) were used for forest (α_f) and meadow (α_m) habitat, respectively.

significantly higher in 1996 than in 1995. Total mortality (within-patch mortality plus mortality of emigrants) was not affected by connectivity; however, estimated mortality occurring during migration decreased greatly with increasing connectivity (Fig. 3). For meadows with the lowest connectivity (S and Z) >90% of emigrants are estimated to have died during migration. The emigration rate (η) was moderate with 1–5% of the individuals leaving a meadow of unit size (1 ha) per day. Emigration and immigration did not scale similarly with habitat size ($\zeta_{em} \neq \zeta_{im}$) measured either as meadow area or *Sedum* abundance. The scaling of immigration increased faster with meadow size than did the scaling of emigration, indicating that large meadows may accumulate migrants. This effect was more pronounced using *Sedum* abundance.

Model goodness-of-fit

Given the limited data, models using meadow area and *Sedum* abundance fit the 1995 data well (Table 4). With the large number of tests we would expect a fraction (5% at $P = 0.05$) to show significant differences (Wahlberg et al. 2002). For the 1995 data, four of 50 tests show lack of fit (using *Sedum* abundance or meadow area), slightly more than the 2.5 that would be expected by chance. There were poor fits for the number of residents in meadows E and G, and for emigrants and immigrants for meadows L and M, respectively. Poor fits for these meadows were found using both meadow area and *Sedum* abundance. Meadows L and M involve a single migrating individual where the predicted value was near zero. For residents in meadow G, the predicted values overestimate the number of residents while the prediction for E is an underestimate. The difference between observed and expected residents may result from sampling. Data used to test goodness-of-fit involve individuals captured on consecutive censuses. There were three consecutive censuses of meadow G. During one of these censuses only three butterflies were captured (compared to 20–30 in other censuses) lowering the observed number of residents. Censuring of the data for goodness-of-fit results in few observations to test the 1996 data, three residents and one movement. Nonetheless, models for 1996, using either *Sedum* abundance or meadow area, predicted individuals to occur in meadows in which observations were made and where dispersal occurred. The goodness-of-fit for models using *Sedum* abundance and meadow area were similar in both years. Goodness-of-fit should be interpreted cautiously as estimation may not be reliable where the predicted number is less than two individuals.

DISCUSSION

The results presented here show an effect of habitat type on the movement of individual butterflies (i.e., forest habitat impedes the migration of *Parnassius smintheus* to a greater degree than does open meadow habitat). These results concur with a previous study of this species. Roland et al. (2000) showed that forest habitat decreased the number of migration events between meadow pairs, indicating that forest may impose an edge effect and an isolation effect that is greater than meadow habitat. Experimental work (J. A. Ross, S. F. Matter, and J. Roland, *unpublished manuscript*), has shown that *P. smintheus* avoid forest edges, and tend to fly less often and at lower rates in forest habitat than in meadow habitat. Much of the difference in behavior in these habitats could be attributed to lower light levels in forest, thereby reducing flight (J. A. Ross, S. F. Matter, and J. Roland, *unpublished manu-*

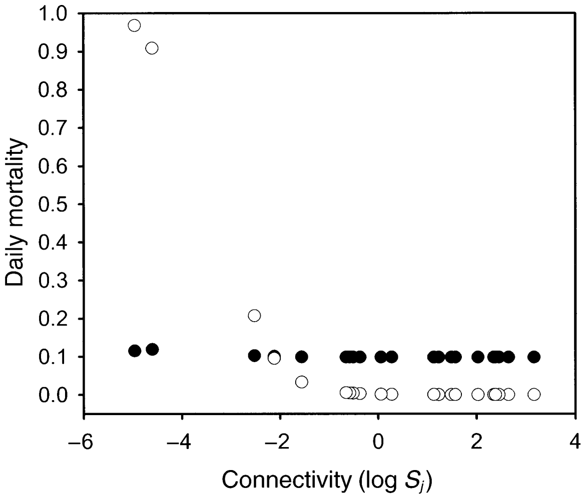

FIG. 3. The relationship between estimated daily mortality of *P. smintheus* and connectivity (S_j). Open circles show the mortality of emigrants from patch *j*, while solid circles show total mortality (within-patch mortality and mortality of emigrants leaving that patch). Daily mortality values are fitted estimates from the model.

TABLE 4. Model goodness-of-fit tests using (A) *Sedum* abundance and (B) meadow area for 1995, with observed (Obs.) and predicted (Pred.) values.

Meadow	Residents				Emigrants				Immigrants			
	Q	df	Obs.	Pred.	*Q*	df	Obs.	Pred.	*Q*	df	Obs.	Pred.
A) *Sedum* abundance												
C	0.00	0	0	0.00	0.00	5	0	0.00	0.00	4	0	0.00
D	1.24	1	14	10.96	0.18	15	0	0.18	1.71	13	1	0.30
d	0.00	0	0	0.00	0.01	15	0	0.01	0.01	10	0	0.01
E	**4.17**	1	28	20.48	1.72	15	1	0.30	0.19	13	0	0.18
F	0.48	1	15	17.46	0.34	18	0	0.34	5.28	19	1	0.20
G	**9.59**	1	6	17.32	8.24	18	2	0.35	1.99	19	1	0.64
g	1.88	1	15	8.35	1.66	13	1	0.32	3.03	17	1	0.23
H	0.00	0	0	0.00	0.02	7	0	0.02	0.00	6	0	0.00
I	0.00	0	0	0.00	0.00	11	0	0.00	0.00	9	0	0.00
J	0.00	0	0	0.00	0.00	9	0	0.00	0.00	10	0	0.00
K	0.00	0	0	0.00	0.00	9	0	0.00	0.00	10	0	0.00
L	0.00	0	0	0.00	**93.75**	11	1	0.01	0.01	12	0	0.01
M	0.10	1	1	0.78	0.00	13	0	0.00	**93.77**	16	1	0.03
N	0.00	0	0	0.00	0.00	0	0	0.00	0.00	0	0	0.00
O	0.00	0	0	0.00	0.01	13	0	0.01	0.00	13	0	0.00
P	0.96	1	0	0.89	13.20	13	1	0.07	0.03	19	0	0.03
Q	1.07	1	0	0.99	0.05	13	0	0.05	13.20	17	1	0.08
R	0.00	0	0	0.00	0.02	11	0	0.02	0.00	12	0	0.00
S	0.00	0	0	0.00	0.00	11	0	0.00	0.00	9	0	0.00
Y	0.33	1	1	1.59	0.06	17	0	0.06	0.01	13	0	0.01
Z	1.85	1	26	21.95	0.02	17	0	0.02	0.03	13	0	0.00
B) Meadow area												
C	0.00	0	0	0.00	0.00	4	0	0.00	0.00	5	0	0.00
D	1.17	1	14	11.04	5.71	13	1	0.14	0.11	15	0	0.11
d	0.00	0	0	0.00	0.11	10	0	0.11	0.01	15	0	0.01
E	**4.08**	1	28	20.55	0.08	13	0	0.07	5.78	15	1	0.20
F	0.50	1	15	17.49	3.34	19	1	0.28	0.23	18	0	0.24
G	**9.61**	1	6	17.32	2.00	19	1	0.45	6.95	18	2	0.40
g	1.92	1	15	8.37	3.70	17	1	0.22	1.91	13	1	0.36
H	0.00	0	0	0.00	0.00	6	0	0.00	0.01	7	0	0.01
I	0.00	0	0	0.00	0.00	9	0	0.00	0.00	11	0	0.00
J	0.00	0	0	0.00	0.00	10	0	0.00	0.00	9	0	0.00
K	0.00	0	0	0.00	0.00	10	0	0.00	0.02	9	0	0.02
L	0.00	0	0	0.00	0.01	12	0	0.01	**83.37**	11	1	0.01
M	0.10	1	1	0.78	**83.40**	16	1	0.03	0.00	13	0	0.00
N	0.00	0	0	0.00	0.00	0	0	0.00	0.00	0	0	0.00
O	0.00	0	0	0.00	0.01	13	0	0.01	0.01	13	0	0.01
P	0.96	1	0	0.89	0.03	19	0	0.03	15.11	13	1	0.07
Q	1.07	1	0	0.99	15.11	17	1	0.07	0.04	13	0	0.04
R	0.00	0	0	0.00	0.01	12	0	0.01	0.01	11	0	0.01
S	0.00	0	0	0.00	0.00	9	0	0.00	0.00	11	0	0.00
Y	0.34	1	1	1.61	0.06	13	0	0.06	0.01	17	0	0.01
Z	1.84	1	26	21.96	0.01	13	0	0.01	0.00	17	0	0.00

Notes: Cases of significant ($P < 0.05$) lack of fit appear in boldface. The data used to test model fit consist only of butterflies that were captured on consecutive censuses.

script). Our present analysis confirms the validity and robustness of the virtual migration (VM) model. The model using a more limited data set captured and quantified these effects. Thus, the VM model can provide useful estimates given few data, which is too often the case for studies of dispersal and threatened species.

Different habitats having independent effects on connectivity has important implications for studies of spatially structured populations. Most models of spatial population dynamics make the assumption that patches are imbedded in a uniform matrix that does not differ in its effect on movement. If matrix types affect migration differently, the application of studies not incorporating these effects may be limited. For example, our estimates of migration and connectivity could have been calculated disregarding matrix type. However, if these estimates were applied in a new location with less forest habitat, we would underpredict the amount of migration. Although the assumption of a uniform effect of the matrix on dispersal has been shown to be adequate for the butterfly *Melitaea cinxia* (Moilanen and Hanski 1998), effects of different matrix habitats on migration have been shown for butterflies (Haddad 1999, Ricketts 2001), other insects (Pither and Taylor 1998, Jonsen et al. 2001), and vertebrates (Joly et al. 2001; but see Bowne et al. 1999). It is clear that the results of any empirical study will depend on the landscape in which it is conducted.

Estimated mortality for *P. smintheus* was moderate in comparison to other butterflies (Wahlberg et al. 2002). Interestingly, within-patch mortality was considerably higher (~8–9%) in 1995 than in 1996. Roland et al. (2000) tested for an effect of year in their analysis of dispersal and found no significant difference between years; however they did not estimate or account for within-patch survival. Predicted mortality during dispersal was strongly affected by connectivity. However, due to the overall low rate of dispersal, total mortality increased only slightly with decreasing connectivity. Although mortality during dispersal strongly decreased with connectivity, our estimate for meadow Z only represents exchanges with other meadows in the system. Meadow Z is part of a large meadow that was not sampled, thus many ''deaths'' may simply have moved to other parts of the meadow. Mortality during dispersal is often neglected in spatial population studies. For small, isolated populations this source of mortality may be especially important (Hanski et al. 2000). For *P. smintheus* at Jumpingpound, populations in small meadows may not be at great risk due to a favorable landscape configuration where most small meadows are close to large ones. Current research is addressing this question.

A potential criticism of our analysis is the use of arbitrary boundaries between contiguous meadows and measuring distance between meadows from centroids of butterfly capture. As such, dispersal could arise from a trivial movement across a boundary, but would be recorded as moving the distance between centroids. Two lines of evidence argue against this being a problem. First, most migrations were not of this sort; migrations originated and ended at positions throughout meadows (Fig. 1). Thus, distances between centroids are a reasonable approximation of mean distance moved. Second, Roland et al. (2000) tested for an effect of artificial boundaries in their analysis. Including a variable coding for whether a meadow was separated by forest or not showed that distance through forest had a reduced, but still significant, effect on movement between meadow pairs. Roland et al. (2000) interpreted this as an edge effect of forest, which has also been shown experimentally (J. A. Ross, S. F. Matter, and J. Roland, *unpublished manuscript*).

Comparisons of models using *Sedum* abundance and meadow area were generally similar. One difference between models using *Sedum* and models using meadow area is in the scaling of immigration with site size. The scaling of immigration with *Sedum* abundance was greater than with meadow area. That is, an increase in *Sedum* abundance would result in a greater increase in the number of immigrants than would a proportional (10 000 plants vs. 1 ha) increase in meadow area. Thus, resources within an area may be more important than area per se. Immigrating *P. smintheus* may be responding to habitat quality (Matter and Roland 2002; but see Matter et al. 2003) rather than to sites as targets (Connor and McCoy 1979). Alternatively, the arrangement of patches may preclude the targets analogy. Meadows tend to be aligned end to end. As butterflies do not move easily through forest, encountering a meadow for a dispersing butterfly may be influenced more by the size of the boundary between meadows rather than by meadow area.

Implications for P. smintheus *and other* Parnassius *species*

Although *P. smintheus* is abundant in the Rocky Mountains, *P. apollo* and *P. mnemosyne* are threatened in Europe (Heath 1981). Probable reasons for the decline of these species, habitat loss and population isolation, are now occurring for *P. smintheus*. Fire suppression and possibly global warming have resulted in a rising tree line, which has reduced meadow area in our study area by >78% since 1952 (Roland et al. 2000). As our study indicates, forest encroachment will result in loss of habitat and decrease the connectivity of local populations. As endangered *Parnassius* species share a similar population structure (Brommer and Fred 1999), the results of this study are relevant to their conservation. This and previous studies of *P. apollo* and *P. smintheus* show that immigration increases with patch quality factors such as nectar flowers, host plants, and mating opportunities (Brommer and Fred 1999, Matter and Roland 2002). However, emigration rates are not higher from low quality habitat than from high quality habitat as might be predicted (Turchin 1991), except where there is a total absence of host plants and correspondingly emigration is very high (Fownes and Roland 2002, Matter and Roland 2002). Given potentially high mortality during emigration, especially in forested areas, conservation efforts would best be directed at conserving remaining habitat and promoting connectivity among existing populations. Creating open, non-forested areas among meadows would increase connectivity for *P. smintheus*.

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