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ALPINE *PARNASSIUS* BUTTERFLY DISPERSAL: EFFECTS OF LANDSCAPE AND POPULATION SIZE

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Abstract. We used mark–recapture methods to estimate the number of *Parnassius smintheus* (Papilionidae) butterflies moving among 20 alpine meadows separated by varying amounts of forest along the east slope of the Rocky Mountains in Alberta, Canada. We combined generalized additive models and generalized linear models to estimate the effects of intervening habitat type and of population size on butterfly movement. By incorporating habitat-specific distances between patches, we were better able to estimate movement compared to a strictly isolation-by-distance model. Our analysis estimated that butterflies move readily through open meadow but that forests are twice as resistant to butterfly movement. Butterflies also tended to stay at sites with high numbers of butterflies, but readily emigrate from sites with small populations. We showed that *P. smintheus* are highly restricted in their movement at even a fine spatial scale, a pattern reflected in concurrent studies of population genetic structure. As an example of the utility of our approach, we used these statistical models, in combination with aerial photographs of the same area taken in 1952, to estimate the degree to which landscape change over a 43-year interval has reduced movement of butterflies among subpopulations. At these sites, alpine meadow habitat has declined in area by 78%, whereas the estimated effect of fragmentation has been to reduce butterfly movement by 41%.

Key words: alpine meadow; butterfly dispersal, connectivity; dispersal; habitat quality; insect; landscape; mark–recapture; Parnassius smintheus; *population size; spatial; tree line; viscosity.*

INTRODUCTION

The effect of distance in limiting dispersal is implicit in the concept of metapopulations, with greater isolation associated with lower probability of dispersal and hence colonization. Treating dispersal as analogous to physical processes such as diffusion, emphasizes strict animal abundance and inter-patch distance but downplays the effect of such biological factors as habitat quality, landscape structure, and connectivity (Taylor et al. 1993). Similarly, modeling metapopulations using only patch size and isolation (e.g., Fahrig and Paloheimo 1987, Hanski and Thomas 1994, Hanski et al. 1994, Hill et al. 1996) may overemphasize the importance of simple euclidian distance, with no estimate of the qualitative nature of the intervening habitat; dispersal may in fact be easier over greater distances through more benign or suitable habitat. Some models of metapopulations have taken into account patch quality, but not of the intervening habitat separating those patches (e.g., Harrison et al. 1988). Similarly, most empirical studies of butterfly movement focus on movement among the patches of suitable habitat, but do not estimate the effects of different intervening habitats (e.g., Watt et al. 1977, Harrison 1989, Thomas et al., 1992, Baguette and Néve 1994, Hanski et al. 1994, Hill et al. 1996, Lewsi et al. 1997). Although studies such as that of the bog fritillary, *Proclossiana eunomia,* have shown that populations are genetically more similar to each other when linked by river courses (wet hay meadows and peat bogs) than are those that are physically closer but unconnected by watersheds (Néve et al. 1996). Such habitat effects are implicit in the potential for habitat corridors linking butterfly populations (Sutcliffe and Thomas 1996). Despite the recognition of the effect of unsuitable habitat on butterfly movement (e.g., Baguette and Néve 1994, Schultz 1997), there are few, if any, quantitative estimates of these effects for inclusion in models of dispersal applied to real landscapes.

One recent exception (Moilanen and Hanski 1998) examined the differences in quality of intervening habitat separating a network of patches inhabited by the butterfly *Melitaea cinxia*. In their study, the effect of intervening habitat was incorporated into the incidence function model (Hanski 1994) by assessing how each habitat type altered the effective distance between patches in the estimation of the isolation of those patches (Moilanen and Hanski 1998). For *M. cinxia,* there was no improvement in the ability of the incidence function model to predict patch occupancy when the effect of intervening habitat type was included; this despite previous experimental work demonstrating that the type of boundary surrounding occupied patches affected their permeability to *M. cinxia* emigration.

Here we use mark–recapture methods to estimate movement of the alpine butterfly *P. smintheus* (Lepi-

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doptera: Papilionidae) through both meadow and forest habitats. In this case, habitat patches (alpine meadows) are arranged in a linear series along mountain ridges, providing a relatively simple landscape with many patches but through which there are only a few possible routes for inter-patch movement. Butterfly species in linear habitats such as mountain ridges, riparian, and coastal habitat, whose movement is partially constrained to one dimension, may exhibit stronger effects of intervening habitat compared to species moving among a two-dimensional network of interlinked habitat patches.

In many alpine areas, the tree line is rising because of the effects of global warming and fire suppression (Grabherr et al. 1994), resulting in smaller and more isolated alpine meadows above the rising tree line as forests fill in lower elevation saddles of alpine meadow. In order to estimate the effects of such landscape change on animal movement, estimates of the effect of separate landscape elements on dispersal needs to be made. We use parameter estimates of movement through meadow and forests respectively to evaluate the net effect of changing landscape on overall dispersal among subpopulations of *P. smintheus* (i.e., change in landscape connectivity, Taylor et al. 1993). We do this for a series of alpine meadows in the Rocky Mountains of Alberta, Canada, which have been rapidly invaded by rising tree line over the past 50 to 60 years. These studies are part of a larger study of butterfly movement, which includes a parallel study of movement based on population genetic structure using DNA microsatellite markers (Keyghobadi et al. 1999).

METHODS

Study site

Studies were conducted in a series of 20 alpine meadows along Jumpingpound Ridge and Lusk Ridge, in the Kananaskis region of Alberta, Canada (51°57′ N, 114°54′ W; Fig. 1). Meadows ranged in size from 0.8 to 26.2 ha in 1993 (Table 1), and each was separated from the next adjacent meadow by between 0 m (two parts of a single large meadow with no intervening forest) and 200 m of intervening forest. Vegetation of the meadows varied, but was generally dominated by grasses, sedges, and mountain avens (*Dryas integrifolia*) and numerous species of wild flowers including the host plant for *P. smintheus*, the lance-leaved stonecrop *Sedum lanceolatum*. Meadows were surrounded by even-aged forests dominated by lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*), with most stands at tree line originating from a large fire in 1938. Tree line in 1996 was at ~2100 m elevation. The size and connectedness of these meadows has changed dramatically over the past 45 years (Fig. 1, Table 1), primarily from the encroachment of forest following the 1938 fire.

Meadow characteristics

Characteristics of each meadow and of the intervening landscape between meadows were estimated from black and white aerial photographs (1 : 40 000 scale) taken in 1952 and in 1993 (Fig. 1). For the recent (1993) photography, we estimated the total distance (kilometers) between each pair of meadows based on the centroids of butterfly captures for each meadow. We also estimated the distance through forest (kilometers) between meadow pairs, and the area of each meadow (hectares). The absolute elevation change in meters between each pair of meadows (down and up) was estimated from topographic maps (1 : 50 000 scale). This was done because in some cases both meadows were at the same elevation, but were separated by a valley. For some of the meadows there was no intervening forest (meadows were actually subsections of larger meadows, Fig. 1), and we therefore assigned an arbitrary boundary line delineating these (Fig. 1 lower panels). These boundaries were not based on resource differences in the separate parts of the meadow, but simply divided the overall area of the meadow into subsections for assignment of butterfly captures. Details of meadow quality are presently under study (Fownes 1999).

The same landscape data were obtained from aerial photographs taken in 1952 (Fig. 1 top, left panel). Because most of the meadows were not separated by forest in 1952, we used the same arbitrary boundaries described above to delineate between adjacent subpopulations. Population size in each meadow was estimated from mark–recapture studies in 1995 and 1996 (see *Methods*: *Mark–recapture*).

Insect

Parnassius smintheus like many Parnassians is typical of mountainous areas. Although some species in the genus are threatened or endangered in other parts of the world (e.g., Heath 1981, Väisänen and Somerma 1985, Bengtsson et al. 1989), *P. smintheus* is one of the more abundant butterfly species on the east slope of the Rocky Mountains of Canada. The host plant, *S. lanceolatum*, tends to grow on dry gravelly sites, particularly on south and southwest-facing slopes just above tree line. Males are very evident as they patrol small territories in search of females, particularly in areas of *S. lanceolatum* abundance. In contrast, females are secretive, flying less than do males, and often crawl in the grass in search of oviposition sites (Scott 1986, Sperling and Kondla 1991). All life stages are thought to be chemically protected from predation by the sequestering of cyanoglucosides from the host plant (Moser and Oertli 1980, Nishida and Rothschild 1995).

Mark–recapture

Our mark–recapture studies served two purposes: to estimate the distances moved by *P. smintheus*, and to estimate population size in each meadow. Each mead-

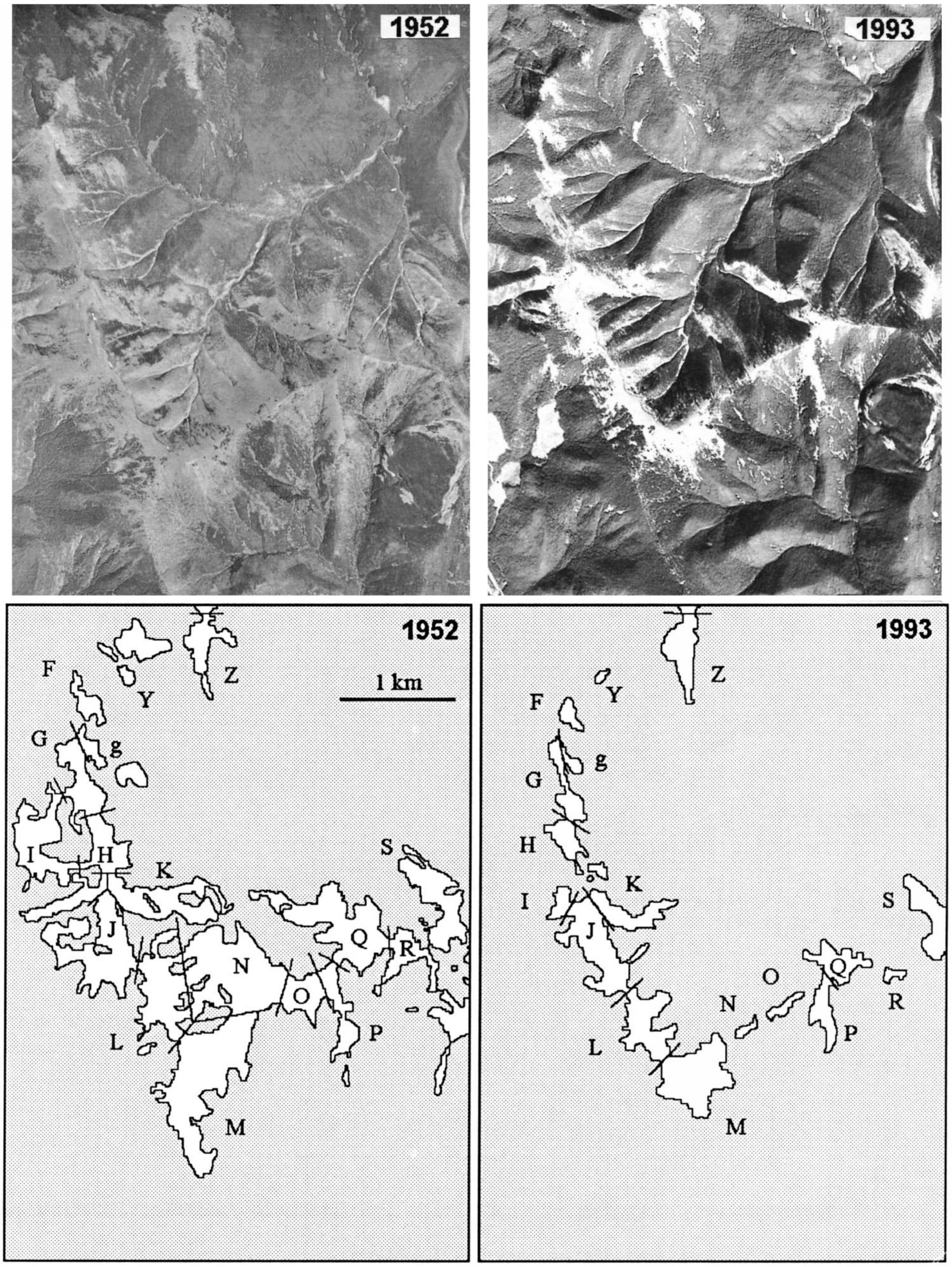

FIG. 1. Meadows of Jumpingpound Ridge, Kananaskis, Alberta. Aerial photos were taken in 1952 (left) and 1993 (right). Schematics of each photo (lower panels) were used to define boundaries between subpopulations (submeadows) used as sample units for the mark–recapture studies. Three additional meadows (D, d, and E) on Lusk Ridge, 3 km to the northwest, are not shown.

ow was sampled three or four times over a five-week period in both 1995 and 1996. In each meadow, individual butterflies were captured by hand net and marked with a three-letter identification code on the ventral side of the hind wing, using a fine-tipped permanent marker. We recorded the sex of the butterfly, the meadow in which they were captured, an *x* and *y* coordinate in meters (from a grid overlain on the aerial photographs), the date, and the time of day. At each subsequent recapture, we recorded the date and time, the three-letter identification code, the *x* and *y* coordinates, and the meadow of recapture. Coordinates on the photographs were assessed to be accurate to ~20 m. Distances that butterflies moved were estimated as the straight-line distance between initial and subsequent capture, but were constrained to routes along the ridgetops given that this species is largely restricted to alpine habitats in this area (Sperling and Kondla 1991).

TABLE 1. Meadow size in 1952 and 1993 estimated from aerial photographs, and population size estimated by Craig's method (Craig 1953) based on mark–recapture data for each meadow.

	Meadow size (ha)		Population size (no.)	
Meadow	1952	1993	1995	1996
D	11.6	8.7	38.0	120.7
d	1.14	1.1	1.2	0.0
E	10.2	9.2	58.3	124.0
F	11.4	3.0	31.6	65.5
G	79.0	8.5	60.0	84.1
g	15.1	2.5	42.4	133.0
H	35.0	3.4	4.0	1.0
I	37.4	4.1	1.0	65.0
J	84.6	26.2	3.0	58.7
K	37.9	8.0	18.3	40.1
L	38.7	18.6	9.0	116.0
M	95.0	25.6	26.5	230.0
N	35.0	1.3	0.0	22.5
O	30.3	2.3	4.3	13.3
P	28.3	7.7	10.0	76.9
Q	63.4	10.2	6.6	102.7
R	20.3	1.3	6.9	36.0
S	45.7	15.1	1.0	13.6
Y	3.4	0.8	5.8	0.0

We estimated population size from the mark–recapture data for each meadow using Craig's method (Craig 1953, Southwood 1978). This method estimates the number of butterflies in the population that are never caught (zero term of an assumed Poisson distribution of captures), and adds it to the number caught at least once. We chose this method because we do not have many multiple captures of individuals, which is required for other methods such as the Jolly-Seber method (Southwood 1978). Estimates were made three to four times during the six-week flight period each year, and were averaged for each meadow in each year. Estimates are therefore best considered as indices of abundance rather than absolute estimates of abundance.

As part of a separate study of genetic structure and of larger scale dispersal of *P. smintheus* using DNA microsatellites (Keyghobadi et al. 1999), we took a clipping of <0.15 cm^2 from one wing of most butterflies in 1995. We were concerned that clipping might affect movement and/or survival, and so, in 1996 we tested for such effects by only clipping every other butterfly at their initial capture. Subsequent movement was compared for clipped and unclipped butterflies in 1996 (Kolmogorov-Smirnov two-sample test), and difference in survival was tested on the distributions of minimum number of days known to be alive (Kolmogorov-Smirnov two-sample test).

Statistical analysis of landscape and movement

We were interested in estimating the effect of type and amount of intervening landscape on the number of butterflies moving between pairs of meadows. Movement was estimated between pairs of meadows to provide data that were directly comparable to genetic distances estimated for the same pairs of meadows (Keyghobadi et al. 1999). The two meadows of each pair were: the ''source'' meadow (where butterflies were originally marked), and the ''target'' meadow where they were subsequently recaptured. Many butterflies were marked and recaptured in the same meadow (i.e., no movement) and so for these ''pairs'' the distance was zero meters. Most butterflies that actually left their source meadow only moved to the immediately adjacent meadow. Because butterflies were marked in all meadows, there was potential for detecting dispersal in both directions between the two meadows of a pair. Due to this, a given section of meadow or forest could be used more than once as an independent variable in the analysis (see *Methods: Problems of lack of independence*). Analysis was restricted to those pairs of meadows satisfying one of two criteria: at least one butterfly moved between the source and the target meadows, or if none had moved to the target meadow, the target had to be adjacent to a meadow to which at least one butterfly had moved. The latter criterion provided some zero counts of recovered butterflies, but reduced the large number of meadow pairs between which no butterflies were recorded as having moved. By imposing these criteria, we reduced the number of pairs of meadows from a maximum possible of 380 in each year ((19 + 18 + . . . + 1) times two directions for each meadow pair) to only 84 in 1995 and 77 in 1996. Because some meadow pairs had other meadows between them, the distance through meadow and through forest between each source and target was the sum of individual segments of each habitat type along the ridgetops.

Model-fitting

We used a combination of generalized additive models (GAM, Hastie and Tibshirani 1990, Preisler et al. 1997) and generalized linear models (GLM, McCullagh and Nelder 1989) with Poisson errors (McCullagh and Nelder 1989) using S-PLUS software (MathSoft 1997) to model the number of recaptures in each target meadow. Cubic B-splines were fit to each variable using generalized additive models because we had no a priori expectation of the shape of the response of the number of recaptures to each variable and because we wanted to test for nonlinearities in each response (Turchin 1998). The best spline-fit model was used as a template against which we compared an alternative parametric model fitting exponential terms within a generalized linear model framework. Detailed criteria used in final model selection are presented in the *Results* section.

The number of *P. smintheus* recaptured for each meadow pair was modeled as a function of: (1) the number marked in the source meadow as a controlling variable for marking effort, (2) the year (1995, 1996), (3) the summed distance (kilometers) through any intervening forest between the two meadows, (4) the summed distance (kilometers) through open meadow between the two meadows, (5) the area (hectares) of the source meadow, (6) the area (hectares) of the target meadow, (7) the estimated population size in the source meadow, (8) the estimated population size in the target meadow, and (9) the cumulative change in elevation (meters, both down and up) between the two meadows.

Problems of lack of independence

The same landscape element (such as distance through a particular section of forest) was used for more than one pair of meadows in the data set, thereby resulting in a lack of independence among some of the variables. Therefore, there is the potential to conclude that regression coefficients are significant, when it is not warranted. For this reason, we also assessed the significance of the observed coefficients using randomization methods (Noreen 1989). The independent variables were shuffled simultaneously and independently, and the regression model refit 1000 times using the GLM procedure. The proportion of these 1000 coefficients for each variable that equaled or exceeded their respective coefficients that were estimated from the original data set were used as an estimate of the probability of obtaining our observed coefficients by chance alone.

Uses of the fitted parametric model

The best-fitting parametric model, which included separate estimates for the effects of distance through forest and distance through open meadow on movement (which we call our LANDSCAPE model) was subsequently used for three purposes. One was to compare to a model with only total distance between meadows (DISTANCE model), which does not separate effects of each of the two habitat types. This is in effect a test of the improvement of the model when resistance to movement in each habitat type is taken into account. The DISTANCE model, therefore, has one less parameter because total distance sums the separate distances through meadow and forest. Another was to predict the actual number of butterflies moving between meadows in 1995 and 1996 instead of just the number of marked butterflies recaptured. This was done by refitting the LANDSCAPE model, but replacing the number marked in the source meadow as an independent variable, with estimated population size for that meadow based on Craig's method (see *Methods: Mark–recapture*). A third was to predict the number of butterflies moving between meadows in 1952 (Fig. 1 top, left panel) when meadows were larger and there was little or no forest between meadows. This was done by reestimating distance through meadow, and distance through forest between meadows for the same area in 1952 aerial photos (Fig. 1). These variables were then fitted to the LANDSCAPE model. Butterfly abundance in each meadow was assumed to be the same in 1952 as it was in 1995 and 1996 because we had no information on what butterfly abundance would have been in the large, early-successional meadows, immediately after the fire had lowered tree line.

RESULTS

Meadow size and population size

Meadows in this study ran along the spine of three adjacent ridges (Fig. 1). In 1952, these meadows varied in size from 1.14 to 95.0 ha (Table 1). The same meadows in 1993 ranged in size from 0.8 to 26.2 ha, averaging only 22% of their size in 1952 (Table 1). Population sizes varied among meadows, depending on meadow size and quality, and were generally higher in 1996 than in 1995 (Table 1), reflecting a general increase in *P. smintheus* abundance since 1993 (J. Roland, *personal observation*).

General movement

Of the 1574 captures in 1995 and 1200 captures in 1996, there were 726 and 445 individual movements (recaptures), respectively, of which there were only 45 and 68 actual inter-patch movements, respectively, in the two years. Although there were very large differences in sample size for the two sexes in both years (Fig. 2), they did not differ in their mean distance moved in either 1995 (males, 131.9 m, SE = 6.06; females, 131.6 m, SE = 21.6; $D_{\max} = 0.138$, $P = 0.62$) or in 1996 (males, 162.4 m, SE = 9.38; females, 118.0 m, SE = 36.72; $D_{\max} = 0.281$, $P = 0.11$). These distances are shorter than the minimum range estimated for male and female *P. phoebus* in Colorado (Scott 1975; males = 195 m, females = 177 m). The longest movements recorded in our study in 1995 and 1996 were 1729 and 1636 m, respectively. Movements were shorter in 1995 than in 1996 (131.9 m vs. 160.6 m, $t = -2.639$, $P = 0.008$) and there were fewer inter-patch movements, possibly because weather was cooler and wetter in 1995.

Clipping of wings did not affect the mean distance moved (Fig. 3; clipped = 159.8 m, SE = 17.1; unclipped = 153.6 m, SE = 9.9, $t = -0.318$, $P = 0.75$), but there were more short movements made by clipped individuals (medians: clipped = 79 m, unclipped = 117 m; $D_{\max} = 0.16$, $P = 0.015$). Despite this, the two longest movements observed in 1996 (1636 and 1621 m) were made by clipped individuals. The number of butterflies actually leaving one meadow and moving to another did not differ for clipped and unclipped butterflies (G test = 0.34, df = 1, $P > 0.60$). These patterns suggest that movement within meadows was affected by clipping but that movement between meadows was not. There was no difference in the minimum number of days known to be alive for clipped and unclipped butterflies (Fig. 4, $D_{\max} = 0.091$, $P = 0.11$).

Detailed model selection

Fitting of the LANDSCAPE model for butterfly mark–recapture data was done in four steps: (1) A gen-

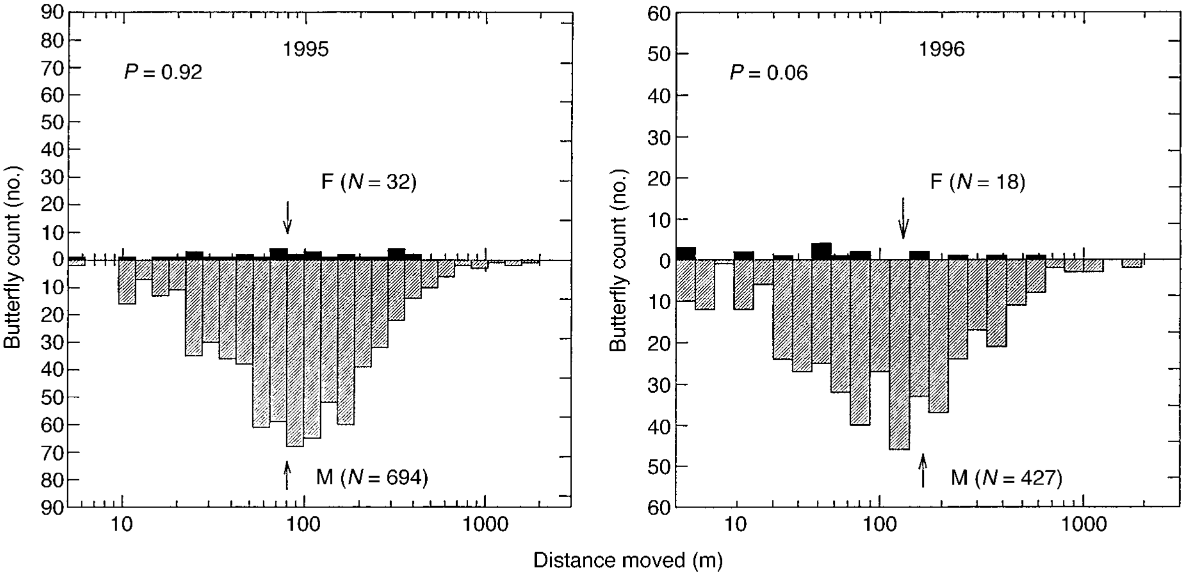

FIG. 2. Distances moved by male (M) and female (F) *P. smintheus* butterflies in 1995 and 1996 (log scale). There was no difference in mean distance moved between captures for the two sexes in either year (see *Results: General movement*).

eralized linear model (GLM in S-PLUS) was fit to the raw data to identify any significant linear predictors among the nine variables (Model 2, Table 2). (2) A nonparametric generalized additive model (GAM in S-PLUS), fitting cubic B-splines, was used to identify any variables that had additional nonlinear effects (Hastie and Tibshirani 1990) in addition to the linear effects (Model 3, Table 2). (3) Because all variables except YEAR had significant nonlinear effects, a parametric model was fitted using natural log-transformed variables in a generalized linear model, thereby estimating the exponential parameter for the effect of each variable (Model 4, Table 2). This nine-variable exponential model was compared to, and found to not differ significantly from, the equivalent nine-variable spline-

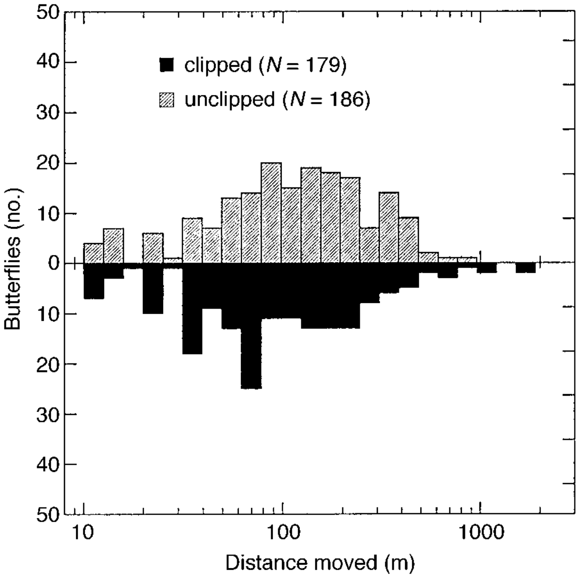

FIG. 3. Distances moved by clipped and unclipped butterflies in 1996 (log scale). Clipping of wings was done to obtain samples for a parallel study of population genetic structure (Keyghobadi et al. 1999). Clipped individuals moved less between captures than did unclipped individuals (medians: clipped = 79 m, unclipped = 117 m; D_{max} = 0.16, P = 0.015), but these differences were primarily within meadows. Numbers moving between meadows did not differ (see *Results: General movement*).

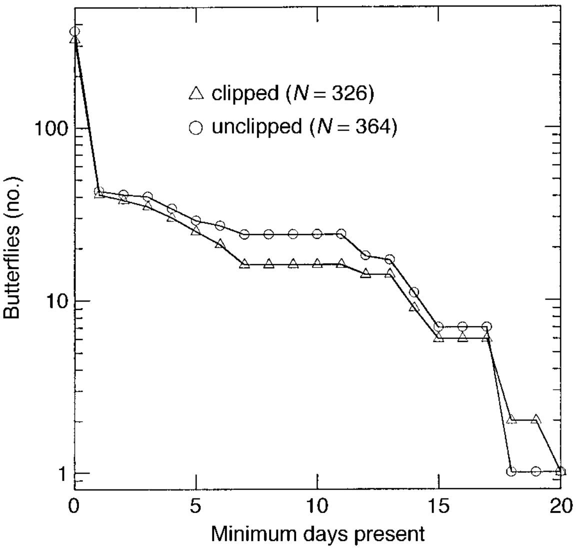

FIG. 4. Minimum known residence times for clipped and unclipped butterflies (log scale). There was no difference in the median residence time between the two groups (D_{max} = 0.091, P = 0.11).

TABLE 2. Residual deviance of alternative generalized linear models (GLM in S-PLUS) and generalized additive models (GAM in S-PLUS) for estimating effects on number of butterflies moving. All models assume a Poisson distribution of errors with dispersion = 1.

Model	Residual deviance	Residual df	Estimated dispersion
1) NULL	4113.03	160	
2) GLM, all nine variables, linear fit	458.82	151	3.04
3) GAM, all nine variables, fitting natural splines	160.07	127.2	1.26
4) GLM, all nine variables, exponential fit	147.37	151	0.97
5) GLM, six significant variables, exponential fit, stepwise forward (LANDSCAPE model)	150.30	154	0.98
6) GAM, six significant variables, fitting natural splines	170.65	136.2	1.25
7) GLM, five variables, exponential fit (DISTANCE model)	171.79	155	1.11

fit model (Table 3), indicating that the exponential form adequately described the nonlinearities in the data. (4) We built the final reduced model using exponential terms for each variable in a stepwise sequence because of the congruence of the exponential GLM model to the spline-fit GAM model. We started with a Null model (intercept only) to which individual terms were added (MathSoft 1997). At each step the best term to add was assessed by the magnitude of the *Cp* statistic estimated for each term (Spector 1994), until no additional terms improved the model. This process resulted in a model with six significant exponential terms: number of butterflies marked, distance through forest between meadow pairs, distance through open meadow, elevation change between meadow pairs, population size in the source meadow, and population size in the target meadow (Model 5, Table 2). There was no effect of area of the source meadow, area of the target meadow, nor of year (1995, 1996) on the number of marked butterflies moving. We call the final six-variable exponential model our LANDSCAPE model because it includes separate effects of forest and meadow on butterfly movement. Like the nine-variable models, the six-variable exponential model did not differ significantly from the corresponding six-variable spline-fit model (Table 3), again confirming the adequacy of the exponential terms in defining the nonlinearities in the response.

Factors affecting butterfly movement

Not surprisingly, the number of butterflies marked in the source meadows had a large effect on the number subsequently recaptured (Table 4, Fig. 5a). This was the first variable to be added in the model; all other terms are therefore assessed after holding the effect of number marked constant.

All three landscape variables (forest, meadow, and elevation change) had significant effects on the number of marked butterflies moving between pairs of meadows (Table 4). The greater the distance through forest between two sites, the lower the number of butterflies recaptured in the respective target meadow (Table 4, Fig. 5b). Similarly, the greater the distance through meadow between two sites, the lower the recapture rate. Recapture rate declined more rapidly, however, through forest (slope = -1.115, Fig. 5b) than it did for an equivalent distance through open meadow (slope = -0.588, Table 4, Fig. 5c). This implies greater viscosity (Wiens et al. 1997) of forest than of open meadow or some combination of viscosity and reluctance by butterflies to enter forests. The two coefficients are significantly different from each other ($t = 2.393$, $P = 0.016$, Sokal and Rohlf 1981). Indeed, we recorded no butterfly recaptures if two sites were separated by >1 km of forest (Fig. 5b). There were fewer butterflies

TABLE 3. Comparisons between alternative statistical models listed in Table 2.

Comparison	Change in deviance	Change in df	*F*	*P*
Null model vs. GLM 9-variable, linear fit, Model 1 vs. Model 2	3667.25	9	14.09	0.0000
Null model vs. GAM 9-variable, spline fit, Model 1 vs. Model 3	3953.36	32.7	74.48	0.0000
GLM nine-variable linear fit vs. GAM nine-variable spline fit, Model 2 vs. Model 3	298.75	23.8	8.09	0.0000
GLM nine-variable exponential fit vs. GAM nine-variable spline fit, Model 4 vs. Model 3	12.70	23.8	0.34	0.99
GLM six-variable exponential fit, (LANDSCAPE model) vs. GAM six-variable spline fit, Model 5 vs. Model 6	20.35	17.8	0.70	0.81
LANDSCAPE six-variable exponential fit vs. DISTANCE five-variable exponential fit, Model 5 vs. Model 7	21.49	1	15.65	0.0001

Notes: Change in deviance between each pair of models is assessed using an *F* test. GLM models are in effect nested within GAM models since the GAM is testing whether there are any additional nonlinear effects (with approximately 3 df for each term), beyond the linear fit. The DISTANCE model is the same as the LANDSCAPE model except that the distances through forest and through meadow between the source and target meadows are simply combined into total distance; hence one less degree of freedom. The *F* is for change in deviance between the two models.

TABLE 4. Model parameters and fit for the LANDSCAPE model (six-variable, exponential fit, Model 5 in Table 2).

Variable	df	Coefficient (SE)	t	P for t test	P* for randomization	Change in deviance	P for χ^2 test on deviance
NULL	160					4113.03	
Intercept		−4.429 (0.52)	−8.25	0.000	0.000		
Number marked	1	1.050 (0.04)	29.66	0.000	0.000	1176.46	0.0000
Distance through forest (km)	1	−1.115 (0.17)	−6.44	0.000	0.000	1686.80	0.0000
Distance through meadow (km)	1	−0.588 (0.14)	−4.35	0.001	0.009	1015.25	0.0000
Elevation change (m)	1	−0.354 (0.05)	−6.50	0.000	0.000	27.38	0.0000
Population size in target meadow	1	0.566 (0.08)	6.87	0.000	0.001	15.14	0.0000
Population size in source meadow	1	−0.556 (0.09)	−6.17	0.000	0.005	40.70	0.0000
Residual deviance	154					150.30	
Dispersion parameter = 0.98.							

Notes: Significant terms were identified using stepwise addition of terms to the NULL model, based on the *Cp* statistic at each step (see *Results: Detailed model/selection*). Coefficients were tested for significance by *t* tests and by randomization methods because of the lack of independence of data from meadow pairs (see *Methods: Problems of lack of independence*). *P** is the significance attained by these randomization tests. Change in deviance of the model by the inclusion of the term is tested against a χ^2 distribution.

recaptured when the target was separated from the source by a large change in elevation (Table 4, Fig. 5d). This suggests, not surprisingly, that larger valleys were greater barriers even after controlling for distance through both forest and meadow.

Butterfly movement was strongly affected by population size. Abundance of butterflies in the source and target meadows affected emigration and immigration, respectively. More butterflies left sites that had small populations (Fig. 5f); and, having emigrated, they were more likely to end up at sites with large populations (Fig. 5e). The two curves for the effect of population

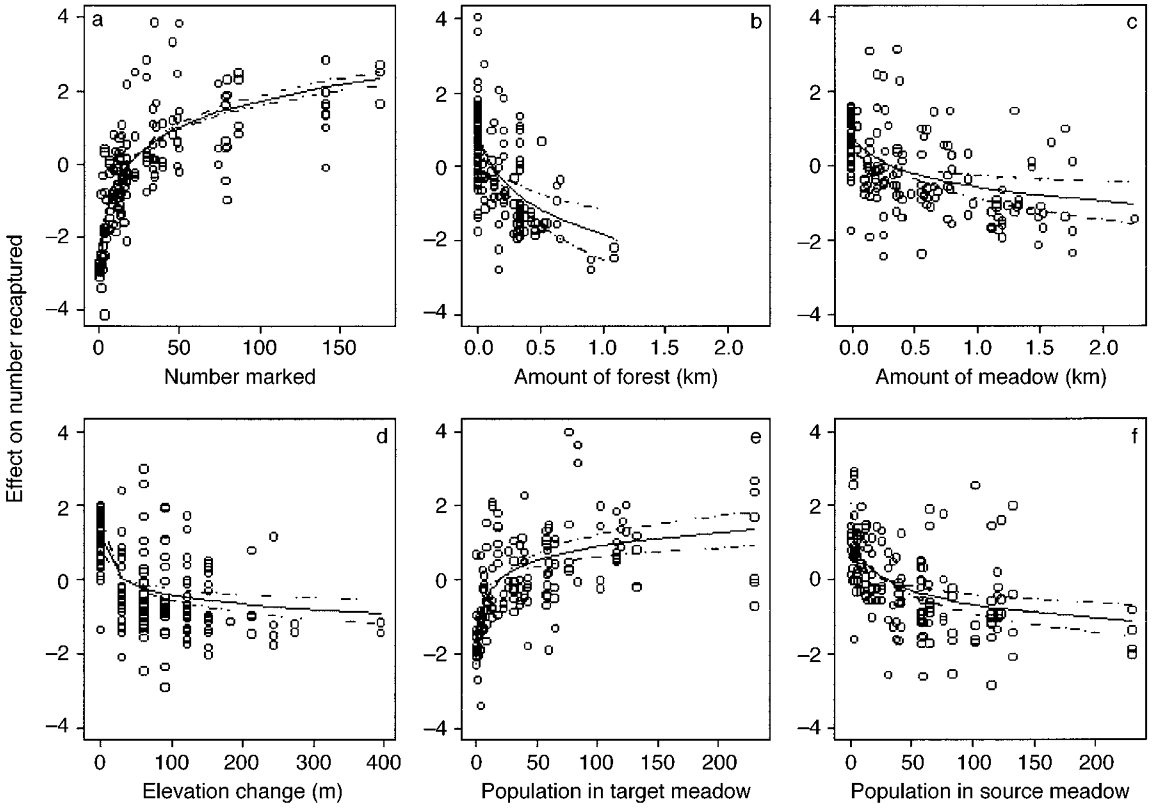

FIG. 5. Effects of number of butterflies marked, intervening habitat, and population size on number of butterflies observed moving to each target meadow based on the LANDSCAPE model. Plots show the additive effect of each variable on the number of butterflies recaptured (coefficients and statistical analysis are presented in Table 4).

size (Fig. 5e and f) are almost exact mirror images of each other, with very similar but opposite coefficients (−0.566 for emigration as a function of density and 0.556 for immigration as a function of density). We did assess whether there were any significant interactions between population size and the amount of forest or meadow on movement, but found none. Therefore, landscape effects on movement were similar regardless of population size, and density effects on movement were similar regardless of intervening landscape, at least over the range of overall high abundances seen in 1995–1996. Size of the source meadow and size of the target meadow did not contribute significantly when added to the model, and were subsequently excluded from it. There was also no effect of year (1995, 1996) on butterfly movement between meadows, and was similarly excluded from the final model.

One aspect of our study design could produce an alternative explanation for greater movement through meadows compared to reduced movement across forests. This potential required some additional analyses. The problem stems from the use of arbitrary boundaries dividing larger continuous meadows into sub-meadows for purposes of mark–recapture (e.g., meadows J, L, and M in Fig. 1 top, right panel). Butterflies in one meadow, crossing our arbitrary boundary, would be recorded as having moved a distance equal to that between the respective centroids of the two patches (i.e., they were estimated to have moved more than they actually did). Estimating movement between centroids would produce similar bias for meadows separated by forest, but the bias would be less since additional movement over the forests would have to occur before being recorded in the next meadow. Therefore, we may have estimated greater movement between the pairs with no intervening forest, simply because of the design. To test for this effect, we added a dummy variable to the final LANDSCAPE model, which coded for whether the two patches were either in the same larger meadow or were indeed separated by forest. The dummy variable entered the model before the other landscape variables. In the resulting analysis, the dummy variable became the most important variable (change in deviance = 1772, df = 1, $P = 0.0000$). Therefore, there was a very large effect of any forest barrier on movement (disregarding actual distance moved) compared to when that barrier was absent. Inclusion of the dummy variable did not change the overall fit of the model (change in residual deviance = 1.06, change in df = 1, $F = 0.78$, $P = 0.38$), but did render the effect of distance through forest much less important, as would be expected since the dummy variable entered the model first. Despite this reduction, distance through forest still had a significant effect (deviance = 4.80, df = 1, $P = 0.028$), suggesting that it is both the presence and size of a forest barrier that reduces *P. smintheus* movement.

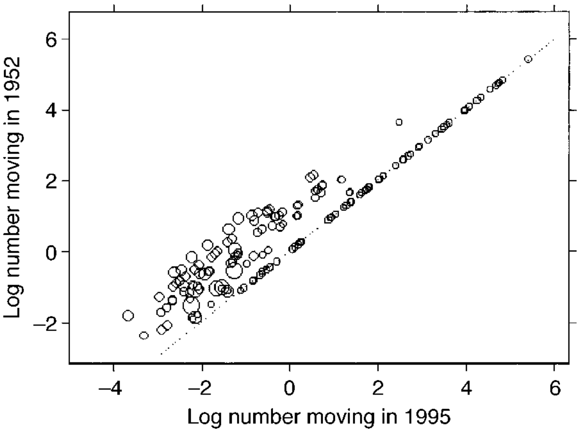

FIG. 6. Estimated number of butterflies moving between pairs of meadows based on the LANDSCAPE model fitted to landscape variables measured from aerial photographs taken of each in 1993 and 1952 (Fig. 1). Size of circles is proportional to the amount of forest between each meadow pair in the 1993 photographs. The diagonal line indicates no change in number moving.

Effect of landscape on movement vs. the effect of simple distance

The six-variable LANDSCAPE model provided a better predictor of butterfly movement than did the five-variable DISTANCE model (Table 3). Therefore, by taking into account resistance of each habitat type separately, we are better able to estimate landscape connectivity for butterfly populations even though the total distances were identical. Having separate parameter estimates for each habitat element in the LANDSCAPE model means that we could predict movement in other landscapes, or estimate movement at the same sites as the proportions of forest and meadow change over time. We illustrate this potential in the next section by comparing the landscape at this site at two points in time, separated by over 40 years.

Movement in 1952 vs. 1995

The actual number of butterflies moving between meadows in 1995 and 1996 was estimated by refitting the LANDSCAPE model, using the population estimate for each meadow as an independent variable instead of using the number marked. This was similarly done using the estimates of the amount of forest and meadow from the 1952 aerial photos (Fig. 1 top, left panel). Connectivity of the landscape, as estimated by the overall movement of butterflies among sites, was much greater in 1952 than in 1995 (Fig. 6). The estimated number of butterflies moving between pairs of meadows declined by 41% overall between 1952 and 1993. In contrast, the average size of the meadows over this interval declined by 78% (Table 1). These two results suggest that, from 1952 to 1993, the rising tree line had a potentially greater effect on loss of habitat than it has had on fragmenting the population and reducing movement.

DISCUSSION

Our results indicate that both landscape structure and population size have significant effects on movement of *P. smintheus* butterflies among sites. Unlike the well studied *Melitaea cinxia* butterfly, for which there is no evidence for landscape effects on patch occupancy, and implicitly on movement (Moilanen and Hanski 1998), our study demonstrates a strong effect of habitat on *P. smintheus* movement, movement that was measured directly. We found that forests are about twice as resistant to butterfly movement than are equivalent amounts of open meadow, a pattern that has the potential to dramatically alter connectivity of these landscapes as forests encroach into alpine meadows. We are encouraged by these results because they reflect, and support, the same pattern of landscape effects on the genetic structure of the same *P. smintheus* populations (Keyghobadi et al. 1999). In the same vein, the fact that the genetic structure of these populations reflects the landscape effects on actual movement shown here, means that dispersing butterflies are successfully reproducing and contributing genes at the sites to which they immigrate. They successfully reproduce after dispersal.

The pattern of fewer recaptures when forest intervenes between meadow patches could arise, alternatively, from greater mortality during dispersal through that habitat. Our analysis cannot tease apart effects on movement vs. those on mortality. Recent modeling approaches (Hanski et al. 2000) have been developed, however, which use recapture histories of individual butterflies moving among patches to estimate rates of movement and mortality separately. This technique is currently being adapted to account for differential movement and mortality in more than one habitat type.

We suspect that part of the reason for our being able to detect landscape effects for *P. smintheus* is that their movement is largely constrained to one dimension; butterflies tend to move along ridgetops with few alternative routes between pairs of meadows. This is in contrast to species such as *M. cinxia* (Hanski 1994) or *Euphydryas editha* (Harrison 1989), which move more typically among a network of patches with more alternative routes among them. Landscape effects on movement might also be readily detected for species that are similarly restricted to linear habitats such as the bog fritillary (*P. eunomia*) in riparian habitats. Support for this comes from the fact that *P. eunomia* populations are genetically more similar to populations connected by water courses compared to populations that are physically closer, but which are not connected by water courses (Néve et al. 1996).

P. smintheus tend to remain in large populations and leave small populations. When they do disperse, they are more likely to end up in sites with large rather than small populations (Table 4; Fig. 5e and f). This pattern of negative density-dependent dispersal is seen for other butterflies, including the fritillaries *M. cinxia* (Kuussaari et al. 1996), *E. editha* (Gilbert and Singer 1973), and *Euphydryas chalcedona* (Brown and Ehrlich 1980). It is unclear whether, for *P. smintheus,* reduced dispersal from large populations results from social interaction among individuals such as that seen for *Euphydryas anicia* (Odendaal et al. 1988), or whether butterfly population size is simply a surrogate of meadow quality, and that butterflies simply move to, and stay in, good meadows. Observational and experimental studies are currently being done to tease these factors apart.

Interestingly, and counter to metapopulation theory, size of meadows had no effect on either emigration or immigration of *P. smintheus*. Although we might expect an effect of perimeter area in causing more emigrants leaving small meadows (Sutcliffe et al. 1997), the constraint of movement along ridgetops may render most of a meadow's perimeter irrelevant; the butterflies primarily encounter the two ends of the meadow as they move along the ridges. Similarly, immigration may be unaffected by patch size since all meadows, regardless of size, would be encountered equally as butterflies move along the ridgetops. This suggests, again, a difference in detecting effects of landscape structure for species inhabiting networks of patches in two dimensions compared to those inhabiting patches arranged in a linear series; the size of a two-dimensional target might be expected to be more important for animals moving in two dimensions than for those whose movement is constrained to one dimension. Conservation and reserve design for species living in linear habitats may consider patch size of less importance than simply number of patches and/or amount of habitat.

The nonsignificance of meadow size may be in part from being positively correlated with population size, and hence the effects of area being obscured in the analysis given that population size is added first to the model. However, when we force area of the target meadow into the model before population size, meadow area causes a change of deviance of only 14.8 (df = 1), and population size still causes a large change in deviance of 365.6 (df = 1). As indicated above, we are currently assessing the interactions between population size and meadow characteristics experimentally to tease these factors apart.

Significance for Parnassius

Unlike *Parnassius* species in many parts of Europe, *P. smintheus* is not a threatened species in the Canadian Rockies. Given the similar size and life histories among *Parnassius* species, the effects of habitat on movement described here for *P. smintheus*, are likely relevant to other members of the genus. An increasing amount of forests along ridgetops in the front ranges of the Canadian Rocky Mountains is reducing the ability of some alpine butterflies to disperse among patches of suitable habitat. *Parnassius smintheus* butterflies disperse along ridgetops covered in forests at a slower rate than through open meadow. As forests have encroached along these ridges over the past half century, the rate of movement has correspondingly declined. Therefore, unlike many models of metapopulations, the simple measure of isolation by distance (Hill et al. 1996) or a weighted estimate of distance (Hanski et al. 1994, Hanski and Thomas 1994) is not as applicable. It is more reasonable to consider the resistance of the individual habitat elements and assess the connectivity of the landscape as the proportions of these elements change. If we had used a purely isolation-by-distance model for *P. smintheus*, there would be no difference in estimates of movement for 1952 and 1995; all meadows would be the same distance apart in both years. Only when we allow for differential viscosity of habitat elements, is there a predicted effect of landscape change on dispersal. However, in fitting our model to data for 1952, we only allowed for change in the landscape variables, not for change in population size in the large, postfire meadows. We did this because we have no estimate of population sizes in 1952, and we do not know whether the larger, early-succession meadows in 1952 were of the same quality as the smaller meadows in 1995. Given the large expanse of meadows in the 1950s (Fig. 1 top, left panel), it is most likely that populations were larger at that time. Our estimate of a greater number of butterflies moving in the 1950s is probably conservative and a higher absolute number of moving butterflies is more likely.

In this study, the main effect of rising tree line from 1952 to 1995 appears to be the loss of habitat (78% loss of meadow) compared to the effect of fragmentation in reducing dispersal (41% fewer butterflies moving). However, this pattern is, in part, the result of the specific sizes and arrangement of our meadows. For example, the presence of small meadows in the center of the chain of meadows (e.g., meadow N, Fig. 1) may have greater effect on overall movement by acting as a stepping stone, than would a small meadow to the side of the main chain (e.g., meadow I). Continued rise in tree line in the future may have greater effects on reducing dispersal than has been seen to date. For example, loss of a few key stepping stones such as meadow Y, N, or R (Fig. 1 top, right panel) despite the minor loss of area, may severely reduce general movement through the chain of meadows. Alternatively, the effects of fragmentation may be lagging behind the effects of habitat loss. Fragmentation could continue to limit movement or even cause extinction in some meadows without any further rise in tree line. This phenomenon illustrates the concept of ''extinction debt'' (Tilman et al. 1994), where equilibrium effects have not yet shown themselves. This is a very likely case in our meadows where, since 1994, populations have been generally increasing (J. Roland, *personal observation*), and many marginal sites may be persisting simply from ''spill-over'' from larger, and higher quality meadows. In years of more normal (lower) density, the fragmentation effects may become more apparent. Long-term monitoring of these meadows will help assess these potential lagged effects.

Significance for other alpine butterflies

Parnassius smintheus is the most abundant butterfly species at our study sites and has been generally increasing in abundance over the past few years. Other species in these meadows may also perceive forests as barriers to movement, and because they are less abundant, the number moving between meadows may be very low indeed. From our models, we predict movement of at least one individual *P. smintheus* per generation for only 11 of the meadow pairs. For a species with 1/10 the population size of *P. smintheus*, and a similar response to landscape, only one pair of meadows (g and G) would be predicted to have at least one individual moving per generation. Such limited movement through the population, support the strong genetic differentiation of *P. smintheus* populations seen even at the fine spatial scale of these populations (Keyghobadi et al. 1999).

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