
Assessing the Roles of Patch Quality, Area, and Isolation in Predicting Metapopulation Dynamics

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Abstract: *Two aspects of patch geometry—area and isolation—currently dominate the field of metapopulation dynamics. Under this area-and-isolation paradigm, models commonly assume that the probability of local extinction decreases as patch area increases and that the probability of colonization increases as patch connectivity increases. Environmental variables other than patch area and isolation are assumed to have relatively little effect on metapopulation dynamics. Our work on a metapopulation of the butterfly *Speyeria nokomis apacheana* highlights the need for a broader view of metapopulation dynamics. In this system, neither occupancy nor turnover patterns were best modeled as functions of patch area or isolation. Instead, other measures of habitat quality explained the most variance in occupancy and turnover. Our study also revealed temporal variation in the factors associated with occupancy and turnover. This variation can cause the results of analyses to vary with the temporal scale of analysis. For example, factors associated with turnover in this system differed among single-year and multiple-year analyses. We emphasize that factors other than patch geometry may drive extinction and colonization processes in metapopulations—especially in systems that experience substantial natural and anthropogenic environmental variability.*

Evaluación del Papel de la Calidad, Área y Aislamiento de Parches en la Predicción de la Dinámica Metapoblacional

Resumen: *Dos aspectos de la geometría de parches —área y aislamiento—dominan actualmente el campo de la dinámica metapoblacional. Bajo este paradigma de “área y aislamiento”, los modelos comúnmente suponen que la probabilidad de una extinción local disminuye si el área del parche aumenta y la probabilidad de colonización aumenta si la conectividad del parche aumenta. Se asume que otras variables ambientales diferentes al área y al aislamiento del parche tienen relativamente poco efecto en la dinámica metapoblacional. Nuestro trabajo en una metapoblación de la mariposa *Speyeria nokomis apacheana* resalta la necesidad de una visión más amplia de las dinámicas metapoblacionales. En este sistema, no se modelaron bien ni la ocupación ni los patrones de rendimiento como funciones del área o aislamiento del parche. Por lo contrario, otras medidas de calidad del hábitat explicaron la mayor parte de la variación en cuanto a ocupación y rendimiento. Nuestro estudio también reveló una variación temporal en los factores asociados con la ocupación y el rendimiento. Esta variación puede hacer que los resultados de los análisis varíen con la escala temporal del análisis. Por ejemplo, los factores asociados con el rendimiento en este sistema discreparon en los análisis entre años individuales y entre años múltiples. Señalamos que factores diferentes a la geometría del parche pueden conducir a procesos de extinción y colonización en metapoblaciones — especialmente en sistemas que experimentan una variabilidad ambiental natural y antropogénica substancial.*

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Introduction

Patch-based models of metapopulation dynamics are designed to efficiently predict patch occupancy, extinction, and colonization of local populations linked by limited dispersal (Hanski & Gilpin 1997; Hanski 1999). Currently, these models focus primarily on the pivotal influences of patch area and isolation (Thomas & Hanski 1997; Hanski 1998; Moilanen 1999). Empirical data and theory usually support assumptions that the probability of local extinction decreases as patch area increases and that the probability of colonization increases as patch connectivity increases (Kindvall & Ahlén 1992; Thomas & Harrison 1992; Thomas et al. 1992; Thomas & Jones 1993; Moilanen et al. 1998). Although ecologists understand that populations may be influenced by many more than two variables, inclusion of environmental variables in addition to patch area and isolation arguably contributes little explanatory power to models of metapopulation dynamics (Hanski 1994; Moilanen & Hanski 1998; but see Sjögren-Gulve & Ray 1996). The area-and-isolation paradigm (Hanski 1998) has been validated by a small group of case studies on plants, vertebrates, and invertebrates (e.g., [Burdon et al. 1985](#); Smith 1980; Verboom et al. 1991; Kindvall & Ahlén 1992; Hanski & Thomas 1994; Eber & Brandl 1996; Moilanen et al. 1998), and butterflies have played a major role in substantiating this paradigm (Hanski 1999).

Despite the frequent and legitimate assumption that patch “geometry” (area and isolation) is the dominant influence on metapopulation dynamics, other measures of habitat quality may also explain significant variance in patch occupancy and turnover (extinction and colonization) (Hanski 1991; Hanski & Thomas 1994; Kindvall 1996; Sjögren-Gulve & Ray 1996; Gyllenberg & Hanski 1997; Harrison & Taylor 1997). Environmental variables such as food resources, topography, and vegetation structure can affect the dynamics of real metapopulations in significant ways (Hanski & Gilpin 1991; Hanski et al. 1994; Singer & Thomas 1996; Thomas et al. 1996; Wahlberg et al. 1996; Harrison et al. 1998; Dennis & Eales 1999; Hanski 1998, 1999; Boughton 1999). If habitat variables other than area and connectivity have significant effects on metapopulation dynamics, then effective management may entail more than simply maintaining a suitable metapopulation geometry. Identifying habitat variables that are associated with patch occupancy and turnover may be especially useful when habitat and matrix qualities are affected by human activities (e.g., Sjögren-Gulve & Ray 1996). Understanding habitat quality and its ramifications for metapopulation dynamics may also clarify whether habitat restoration will be an effective management tool.

Our research on the butterfly *Speyeria nokomis apacheana* (*S. nokomis*) addresses the relative influence of patch geometry and other patch variables on metapopulation dynamics. This research was initially motivated

by the species’ rarity and by threats to remaining populations from urbanization and agricultural activities (Britten et al. 1994). *S. nokomis* occupies seeps, springs, and riparian areas in the otherwise xeric Great Basin of North America. In desert landscapes, riparian areas attract disproportionately heavy use from numerous faunal groups, including humans. Thus, both riparian communities and *S. nokomis* are management priorities in the region (Kauffman & Krueger 1984; Armour et al. 1991; Thomas 1991; Dawson 1992). Changes in the quality of riparian habitat might have significant effects on the metapopulation dynamics of this riparian-obligate butterfly. To test this hypothesis, we identified a metapopulation of *S. nokomis* that meets criteria necessary for modeling patch dynamics (Hanski 1994). This metapopulation includes a number of habitat patches (39), intermediate patch occupancy (33–90% over 6 years), and substantial observed turnover (17 colonizations and 31 extinctions). We used 6 years of data from this metapopulation to develop separate models of patch occupancy and population turnover. For each model, we explored patch area, isolation, and other measures of habitat quality as predictive variables.

Choice and parameterization of metapopulation-occupancy models can be complicated by numerous factors (Hanski 1999; Moilanen 2000; Sjögren-Gulve & Hanski 2000). For example, “state-transition” models require a sufficient number of observed turnover events for satisfactory parameterization (Sjögren-Gulve & Ray 1996; Sjögren-Gulve & Hanski 2000). To yield accurate predictions, these observed turnover events also need to be representative of turnover patterns over time (e.g., Hanski 1999; Moilanen 2000). A single snapshot of patch occupancy is ostensibly adequate to parameterize some metapopulation models, including the incidence-function model (Hanski 1994, 1999), but parameters based on multiple years of data are expected to yield more-accurate predictions (Hanski 1994, 1999; Moilanen 1999). To assess how models of patch occupancy and population turnover may be influenced by the period over which data are gathered, we also used the *S. nokomis* system to examine temporal patterns of metapopulation dynamics. We tested whether the same environmental factors were associated with turnover in different years and whether variables associated with turnover in 1 year were also significant in analyses that included data from multiple years.

Methods

Field Methods

We considered a patch suitable for *S. nokomis* if its larval host plant (the violet *Viola nephrophylla*) and adult nectar sources (several species of thistles in the genera

Cirsium and *Carduus*) were both present in the patch. Patches of suitable habitat were located in a comprehensive survey of the Toiyabe Range (Lander and Nye counties, Nevada, U.S.A.), a mountain range in the central Great Basin. All accessible springs, seeps, and riparian areas within 30 drainages were surveyed for suitable habitat. A small percentage of suitable habitat may occur on inaccessible private lands, which cover approximately 2% of the Toiyabe Range. Using topographic and hydrologic maps from the U.S. Geological Survey, we estimated that inaccessible drainages harbor negligible amounts of suitable habitat. We used differentially corrected global positioning system (GPS) coordinates to map and calculate the geometric attributes of each patch. Patch coordinates, perimeter, and area were derived by overlaying GPS positions on a 30-m digital elevation model maintained on a geographic information system. There is often an abrupt transition between the wet meadows that can support *S. nokomis* and the surrounding dry-meadow or sagebrush-dominated vegetation. Therefore, patch boundaries were generally easily delineated.

For each year from 1995 to 1999, patch status was determined by experienced observers visiting each patch repeatedly during weather conditions suitable for butterfly flight. *Speyeria nokomis* are among the largest and most visually striking butterflies in the Great Basin. They are strong fliers, and individual adults often live for several weeks (E.F., unpublished data). Thus, it is highly unlikely that we failed to detect the species in a patch where it actually was present. The status of each patch was classified each year as 0, not occupied; 1, occupied; E, previously occupied but now extinct; or C, previously unoccupied but now colonized (Sjögren-Gulve & Ray 1996). We used the presence of adults to determine occupancy, because cryptic larvae, low larval densities, and inaccessibility of the study area during much of the year made it virtually impossible to search for juvenile life stages.

Data on population size and dispersal were obtained from mark-release-recapture studies. During the 1995–1998 field seasons, we captured, marked, and recaptured *S. nokomis* in each habitat patch according to standard methods (Ehrlich & Davidson 1960; Watt et al. 1977). We gave each butterfly a unique mark on the underside of its wings that was cross-referenced to the date and location of capture or recapture. The sex of each butterfly was recorded. We used analysis of variance ($\alpha = 0.05$) to test whether mean number of captures, recaptures, or dispersers varied by year and whether mean dispersal distances varied by year or by sex. When there was a significant difference among all years, we used Tukey–Kramer HSD tests to compare pairs of means. We also tested whether the number of captures could be explained as a function of patch area. Low abundances prevented us from making meaningful estimates of annual patch-level population sizes with Jolly-Seber, Lincoln, or

other common mark-recapture algorithms. On the basis of our field methods and the life-history characteristics of *S. nokomis*, however, we believe that number of captures is an accurate index of population size in our study system.

Plant composition and structure affect butterflies both directly and indirectly and could function as key components of habitat quality. During the 1996 flight season, we measured eight vegetation variables in each patch (Table 1): abundance of host plants and thistles; percent cover of host plants, thistles, live vegetation, bare ground, and litter; and vegetation height. Data were collected from 1-m² quadrats spaced evenly throughout each patch. In most patches, the number of quadrats sampled was proportional to patch area. If patch area was <1 ha, we sampled 1 m² per 100 m² of habitat; if patch area was >1 ha, we sampled 1 m² per 500 m² of habitat. Abundance was recorded as the midpoint of one of four abundance classes (1–3, 4–10, 11–30, 31–100) and averaged across all quadrats sampled (Fleishman et al. 1996). Percent cover (percentage of quadrat area covered) was recorded as the midpoint of one of 12 percent-cover classes (0–0.99, 1–4.99, 5–14.99, 15–24.99, . . . , 95–100) and averaged across all quadrats sampled. In no instance did cover exceed 100%. Bare ground was defined as area not covered by live vegetation or litter. Litter was defined as all dead vegetation, either rooted or not rooted. Vegetation height was rounded to the nearest 0.1 m and included both live and standing dead vegetation.

We also surveyed the presence of native and non-native thistles and the magnitude of human-generated disturbance in each patch. Two species of thistles, *Carduus nutans* and *Cirsium vulgare*, are not native to the Great Basin and are generally regarded as noxious weeds. Two additional species, *Cirsium scariosum* and *C. neomexicanum*, are native to the Great Basin. For each year from 1995 to 1998, we categorized human-generated disturbance, including livestock grazing and recreational use, in each patch as 0, minimal; 1, moderate; or 2, heavy.

The proximity of occupied patches or extinction sites may affect dynamics in a focal patch. Therefore, we recorded data on the proximity and density of occupied patches and extinction sites for each patch in each year. To allow for the time-lagged effect of occupancy in one patch on occupancy in its neighbor, we considered a neighboring patch “occupied” if it was occupied in the previous survey. We considered a neighboring patch an “extinction site” if it was occupied in the previous survey and unoccupied in the current survey. For each patch in each year from 1995 to 1999, we determined distances to the nearest occupied patch and nearest extinction site. We also calculated the yearly number of occupied patches and extinction sites within a 4-km radius of each patch. Our mark-recapture data indicate that *S. nokomis* routinely disperses up to 4 km from its natal patch; we recorded only one instance of dispersal further than 4 km.

Table 1. Measures of habitat quality included in models of *Speyeria nokomis apacheana* metapopulation dynamics.

Variable	Description
HOSTct	number of larval hostplants (the violet <i>Viola nephrophylla</i>)
NECTct	number of adult nectar sources (various species of thistles; see below)
HOSTcov	percent cover of larval hostplants
NECTcov	percent cover of thistles
TVC	percent cover of live vegetation
LITTER	percent cover of dead vegetation
BARE	percentage of ground not covered by live vegetation or litter
VEGht	mean height of live and standing dead vegetation
CANU	presence (1) or absence (0) of the thistle <i>Carduus nutans</i>
CIVU	presence (1) or absence (0) of the thistle <i>Cirsium vulgare</i>
CISC	presence (1) or absence (0) of the thistle <i>Cirsium scariosum</i>
CINE	presence (1) or absence (0) of the thistle <i>Cirsium neomexicanum</i>
DISTURB	human-generated disturbance (including livestock grazing and recreational use) for each year between 1995 and 1999, categorized as minimal (0), moderate (1), or heavy (2)
UTMX	latitudinal coordinate (universal transverse mercator units)
UTMY	longitudinal coordinate (universal transverse mercator units)
PERIM	perimeter in meters
AREA	log _e area in square meters
Docc	distance in meters to the closest occupied patch for each year between 1996 and 1999, taken from surveys in the preceding year
Dext	distance in meters to the closest neighboring extinct patch for each year between 1995 and 1999, taken from same-year surveys
Nocc	number of occupied patches within a 4-km radius for each year between 1996 and 1999, taken from surveys in the preceding year
Next	number of extinct patches within a 4-km radius for each year between 1995 and 1999, taken from same-year surveys

Analyses

Because we not only observed a relatively large number of extinctions and colonizations but also had substantial data on habitat quality, we used multiple logistic regression to identify the best correlates (covariates) of occupancy and turnover (Hosmer & Lemeshow 1989; Sjögren-Gulve & Ray 1996). Patch occupancy, extinction, and colonization were modeled separately as binary responses to one or more explanatory environmental variables. Explanatory variables (the covariates) included in logistic regression may be either continuous or categorical (nominal, ordinal, or binary). We constructed five separate single-year occupancy models, four single-year and two multiple-year extinction models, and two single-year and two multiple-year colonization models. In two of our study years, the number of colonizations was not sufficient for analysis.

Models were built according to a forward stepwise selection procedure (Hosmer & Lemeshow 1989) starting with the constant and all explanatory variables outside the model (step 0; Sjögren-Gulve & Ray 1996). Stepwise multiple regression selects the subset of explanatory variables that improves the accuracy of the logistic model to the greatest extent. This selection procedure enters variables into the model one at a time. At each step, the improvement chi square value of each entered variable is evaluated, and variables that do not significantly improve model fit are dropped. We used a critical significance level of 0.10 for entering a variable into or removing a

variable from the model. Applying a more stringent critical significance level (e.g., 0.05) might exclude variables that could greatly improve the explanatory power of the models (e.g., Sjögren-Gulve & Ray 1996; see also Hosmer & Lemeshow 1989; Pearce & Ferrier 2000).

Because we had several years of data, we could construct several different models for each response variable. Often in such cases, significance levels are adjusted for the number of models constructed (e.g., with Bonferroni corrections), but most metapopulation studies yield only enough data to produce a single model for each response variable. Because our goals were to mimic this data limitation and to avoid Type II errors while illustrating how the period of data collection may affect models, we did not apply Bonferroni corrections (see Pearce & Ferrier 2000). Although this decision increased the risk of obtaining a spurious correlation (Type I error), it increased our confidence that variables that were not significant in any analysis were not the most useful predictors of metapopulation dynamics. Therefore, we simply applied caution when interpreting the significance level for each variable included in the final models.

Some of the measures of habitat quality we included in our models (Table 1) may be correlated. However, because the step selections in our analyses were forward and based on maximum-likelihood ratios with individual assessments of model improvement for each variable (Hosmer & Lemeshow 1989), correlations between explanatory variables did not inhibit identification of the

Table 2. Annual occupancy and turnover in the Toiyabe Range metapopulation of *Speyeria nokomis apacheana*.*

Year(s)	Occupancy	Turnover	Extinctions	Colonizations
1995	0.90 (35)	0.10 (4)		
1996	0.67 (26)	0.28 (11)	10	1
1997	0.33 (13)	0.49 (19)	16	3
1998	0.46 (18)	0.38 (15)	5	10
1999	0.33 (13)	0.33 (13)	9	4
1995–1998	0.59 (23)	0.31 (12)	30	14
1995–1999	0.54 (21)	0.32 (12)	31	19

*Occupancy and turnover are presented as proportions of the total number of patches, with number of patches in parentheses. Extinctions and colonizations are presented as number of patches. One patch was colonized twice. The analysis of colonizations between 1995 and 1999 included two patches known to have been vacant in 1994 that were occupied in 1995.

“best” covariates or predictors of the observed responses. Furthermore, temporal correlation among potential explanatory variables in multiple-year analyses did not introduce a mechanism for masking the potential contribution of such variables, because we assumed that explanatory variables had an instantaneous effect on the response variable (Ter Braak et al. 1998).

Results

Metapopulation Structure

We located and delineated 39 patches of suitable habitat for *S. nokomis* in the Toiyabe Range. Patch area varied from 1 to 8 ha (1.8 ± 2.6 ha, mean \pm SD). The minimum distance between a given patch and its nearest neighbor was 0.5 ± 0.7 km, which fell within the average dispersal distance of emigrant *S. nokomis*.

Between 1995 and 1998, we captured 456 individual *S. nokomis*. Of these, 181 (40%) were recaptured. This is a relatively high recapture rate for a long-term butterfly study (Brussard & Ehrlich 1970; Ehrlich & Gilbert 1973; Watt et al. 1979; Boggs 1987). Of the recaptured butterflies, 47 (26%) emigrated from the patch where they were captured initially. The remaining 74% were recaptured, often repeatedly, in the same patch. Net linear-dispersal distances ranged from <100 to >4500 m (mean = 1.0 ± 1.2 km). Neither year ($F_{3,58} = 0.17$, $p = 0.92$) nor sex ($F_{1,58} = 0.07$, $p = 0.79$) had a significant effect on dispersal distance.

There was considerable spatial and temporal variation in butterfly abundance. The maximum number of butterflies captured in one year in one patch was 69. Year had a statistically significant effect on number of captures ($F_{3,151} = 7.60$, $p < 0.0001$). Significantly more butterflies were captured in 1995 than in 1997 or 1998, but neither the ratio of recaptures to captures ($F_{3,83} = 1.42$, $p = 0.24$) nor the ratio of emigrants to recaptures ($F_{3,47} = 1.12$, $p = 0.35$) varied significantly among years. If actual abundances were double or even triple the number of butterflies we captured, most patches would still have had population sizes well below 100 butterflies in most

years. Number of captures was a significant ($p \leq 0.05$) function of patch area in only one year (1995: $F_{1,38} = 4.50$, $p < 0.05$).

Metapopulation Dynamics: Occupancy and Turnover

Between 1995 and 1999, the proportion of patches occupied each year ranged between 0.33 and 0.90 (0.54 ± 0.24) (Table 2). Annual turnover varied from 0.10 to 0.49 (0.32 ± 0.14) of the patches. The status of eight patches (21%) did not change: 2 remained vacant and 6 were occupied continually. Thirty-one patches went extinct and 17 were colonized between 1996 and 1999. Seventeen patches experienced both state transitions.

Occupancy

We ran five separate single-year occupancy analyses (Table 3). The goodness-of-fit statistic for each final model quantifies the deviation between predicted and observed responses across all patches in the analysis. A high goodness-of-fit p value means that relatively little deviance exists between predicted and observed patch states (Hosmer & Lemeshow 1989). The 1995 and 1996 models each yielded predictions of patch status with a goodness-of-fit p of >0.5 . Annual patch classifications based upon the 1997, 1998, and 1999 models were less accurate (each model had a goodness-of-fit p of <0.5).

Neither area nor isolation entered any occupancy model (Table 3). Isolation was significantly correlated with patch occupancy in step 0 of the model selection in one of the five analyses, but 13 other explanatory variables had higher improvement chi-square values. Area was significant ($p < 0.10$) in four of the five analyses, but four or more other variables had higher improvement chi-square values. Eight other variables were significant in at least one final occupancy model. Probability of occupancy increased with increasing larval host-plant abundance and percent cover of thistles (adult nectar sources), and with the presence of the native thistles *Cirsium scariosum* and *C. neomexicanum*. Probability of occupancy decreased with increasing cover of litter (dead vegetation) and, with

Table 3. Occupancy models and relative degree of model improvement (improvement χ^2)^a of the significant predictors of occupancy in each final model for *Speyeria nokomis apacheana*.

Year	Goodness of fit ^b	U_{occ} ^{c,d}	Significant variables ^d	Improvement χ^2 ^e (p)
1995	0.998	1.1 NECTcov + 99.85 CISC	NECTcov CISC	16.42 (≤ 0.001) 4.86 (≤ 0.05)
1996	0.844	2.187 HOSTct - 1.497 DISTURB94	HOSTct DISTURB94	25.56 (≤ 0.001) 7.70 (≤ 0.01)
1997	0.251	-1.31 DISTURB95	DISTURB95	10.62 (≤ 0.01)
1998	0.378	-2.717 DISTURB95 + 2.034 DISTURB96 - 0.1093 LITTER + 0.5327 NECTcov	DISTURB95 DISTURB96 LITTER	12.93 (≤ 0.001) 10.16 (≤ 0.01) 7.31 (≤ 0.01)
1999	0.389	-1.540 DISTURB95 + 101.4 CINE	NECTcov DISTURB95 CINE	5.49 (≤ 0.05) 12.51 (≤ 0.001) 4.66 (≤ 0.05)

^aAll chi-square statistics have one degree of freedom.

^bDeviance goodness-of-fit p value of the final model. A high goodness of fit means that there was relatively little deviance between predicted and observed patch states (Hosmer & Lemeshow 1989).

^cOccupancy logit.

^dVariables are defined in Table 1.

^eImprovement chi-square p value from the final logistic regression model.

one exception, human-generated disturbance. Between one and four variables were included in each occupancy model. Thistle cover entered two models and disturbance entered four models.

EXTINCTION

Single- and multiple-year extinction models are shown in Table 4. We performed four single-year and two multi-

ple-year analyses. We tested whether addition (or exclusion) of a single year could alter a multiple-year analysis by including either 3 or 4 years of observed extinctions in our multiple-year analyses. We constructed one model with data from 1995–1998 and one with data from 1995–1999. The status of 13 patches (33%) changed between 1998 and 1999, although summary statistics on occupancy, turnover, and extinction appear quite similar between those years (Table 2). Multiple-year extinction

Table 4. Extinction models and relative degree of model improvement (improvement χ^2)^a of the significant predictors of extinction in each final model for *Speyeria nokomis apacheana*.

Between years	Goodness of fit ^b	U_{ext} ^{c,d}	Significant variables ^d	Improvement χ^2 ^e (p)
1995-1996	0.993	-3.766 HOSTct + 0.1514 LITTER - 3.727 CIVU - 0.0007325 Dext96	HOSTct LITTER CIVU Dext96	17.07 (≤ 0.001) 12.32 (≤ 0.001) 5.59 (≤ 0.05) 3.39 (≤ 0.10)
1996-1997	0.251	1.462 DISTURB95	DISTURB95	6.72 (≤ 0.01)
1997-1998	0.592	-1.045 DISTURB96	DISTURB96	12.03 (≤ 0.001)
1998-1999	0.715	7.266 DISTURB98 - 202.9 CINE - 1.047 Next98 - 22.67 VEGht	DISTURB98 CINE Next98 VEGht	11.06 (≤ 0.001) 7.63 (≤ 0.01) 4.96 (≤ 0.05) 4.26 (≤ 0.05)
1995-1998	1.000	-0.09838 Dext - 162.1 CINE + 9.191 LITTER + 1.3 TVC	Dext CINE LITTER TVC	33.62 (≤ 0.001) 10.15 (≤ 0.01) 9.89 (≤ 0.01) 7.24 (≤ 0.01)
1995-1999	0.870	0.1281 LITTER - 2.404 CISC	LITTER CISC	23.77 (≤ 0.001) 6.12 (≤ 0.05)

^aAll chi-square statistics have one degree of freedom.

^bDeviance goodness-of-fit p value of the final model. A high goodness of fit means that there was relatively little deviance between predicted and observed patch state transitions (Hosmer & Lemeshow 1989).

^cExtinction logit (Sjögren-Gulve & Ray 1996).

^dVariables are defined in Table 1.

^eImprovement chi-square p value from the final logistic regression model.

models tended to have higher goodness-of-fit statistics than single-year models. Thus, our extinction analyses provide some support for the hypothesis that models parameterized with multiple years of turnover data predict observed extinctions more accurately than those parameterized with only 1 year of data (Hanski et al. 1996; Hanski 1999; Moilanen 1999).

Ten distinct variables were included in the single-year extinction models (Table 4). Probability of local extinction increased with increasing percent cover of litter and disturbance. Probability of extinction decreased with increasing larval host-plant abundance, presence of the adult nectar sources *Cirsium vulgare* or *C. neomexicanum*, increasing vegetation height, distance to the nearest recent extinction, and number of nearby extinctions. Only the latter relationship is not intuitive. Disturbance (in 1995, 1996, or 1998) was the only variable included in more than one model. Patch area, perimeter, and isolation (distance to nearest occupied patch) all failed to enter these models. In step 0 of the stepwise selection, isolation was significant in two of the six analyses, but eight or more other variables had higher improvement chi-square values. Area was significant in step 0 in four of the six analyses, but five or more other variables had higher improvement chi-square values.

Just three of the environmental variables included in the single-year extinction models—litter, presence of the native thistle *C. neomexicanum*, and distance to the nearest extinct population—were significant in one or both multiple-year analyses. In the multiple-year models, probability of extinction also increased with increasing vegetation cover and decreased with presence of the native thistle *C. scariosum*. Litter was the only habitat variable common to both multiple-year extinction models, illustrating that a single year (1998–1999, in this case) can have a strong impact on a multiple-year analysis.

COLONIZATION

Single- and multiple-year colonization models are presented in Table 5. We performed only two single-year

analyses, because sample sizes (number of colonizations) for the remaining years were quite small (Table 2). The single-year colonization models tended to have higher goodness-of-fit p values than the multiple-year models. This result implies that the determinants of colonization may vary between years so that the predictive power of models based on several years will be relatively low.

Isolation did not enter any of the final single- or multiple-year colonization models. At least 14 other variables had higher improvement chi-square values. Area was significant in step 0 in two of the four analyses, but it was preceded in significance level by four or more other variables. Three variables, percent cover of larval host-plants and disturbance (1995 or 1997), entered the single-year colonization models. Probability of colonization increased with host-plant cover and decreased with disturbance.

Although disturbance (in different years) was significant in both single-year models, it did not enter either multiple-year model. In the multiple-year models, probability of colonization increased with increasing larval host-plant cover or abundance and with the presence of *Cirsium vulgare*. Some measure of host-plant availability entered one single-year model and both multiple-year models. Presence of *C. vulgare* was significant in just one of the pooled colonization models, reiterating that a single year's data can alter a multiple-year model.

Discussion

Metapopulation Structure

Real systems rarely match the purely theoretical definitions proposed for metapopulations (Harrison & Taylor 1997). The main reasons to label a system as a metapopulation, or a particular type of metapopulation, are to provide a general frame of reference and to suggest a relevant modeling framework. Our mark-recapture and occupancy data suggest that, in the Toiyabe Range, *S. nokomis* forms many small and ephemeral populations, with some resem-

Table 5. Colonization models and relative degree of model improvement (improvement χ^2)^a of the significant predictors of colonization in each final model for *Speyeria nokomis apacheana*.

Between years	Goodness of fit ^b	U_{col} ^{c,d}	Significant variables	Improvement χ^2 ^e (p)
1997–1998	0.176	–0.9322	DISTURB95	5.94 (≤ 0.05)
1998–1999	0.914	–2.207	DISTURB97 + 0.2869 HOSTcov	20.37 (≤ 0.001) 2.71 (≤ 0.10)
1995–1998	0.624	0.6282	HOSTct + 100 CIVU	5.61 (≤ 0.05) 5.10 (≤ 0.05)
1995–1999	0.142	0.2493	HOSTcov	5.15 (≤ 0.05)

^aAll chi-square statistics have one degree of freedom.

^bDeviance goodness-of-fit p value of the final model. A high goodness of fit means that there was relatively little deviance between predicted and observed patch state transitions (Hosmer & Lemeshow 1989).

^cColonization logit (Sjögren-Gulve & Ray 1996).

^dVariables are defined in Table 1.

^eImprovement chi-square p value from the final logistic regression model.

blance to a “classical” metapopulation (Harrison 1991; Hanski 1994; Hanski & Thomas 1994; Hanski et al. 1995). We base this characterization on four criteria (Hanski 1999). First, our emigration data suggest that individual patches of habitat support distinct breeding populations. Second, with abundances generally lower than 50–100 butterflies, no individual population seems sufficiently large to ensure the long-term persistence of the metapopulation. Third, recolonization is frequent, yet not all suitable habitat is occupied continually. Almost half (44%) the patches were colonized or recolonized between 1995 and 1999; several had been vacant for more than one year. Finally, the dynamics of local populations are not strongly coupled: in each year we observed colonizations, extinctions, and both increases and decreases in local abundance.

One apparent inconsistency between the dynamics of this system and those proposed in classical metapopulation models is that patches in this system differ in quality, but these differences in patch quality do not appear to cause a significant deviation from classical dynamics. For example, the metapopulation clearly does not have a “mainland-island” structure: no single patch can guarantee its long-term persistence (cf. Harrison et al. 1988). Neither is it a “source-sink” system. In certain spatial clusters of patches, some populations may episodically function as local sources or sinks. But differences in patch quality do not appear to confer permanent or system-wide source or sink status on those patches. For example, five of the nine populations that fell within the top abundance decile in one or more years became extinct at least once. Differences in habitat quality seem to influence the proportion of time one would expect each patch to be occupied, rather than the persistence or productivity of populations.

Habitat Quality and Metapopulation Dynamics

Our study demonstrates that patch quality can supersede patch geometry as an explanation for metapopulation dynamics. Although *S. nokomis* lies toward the classic end of the metapopulation structure continuum (Harrison & Taylor 1997; Thomas & Hanski 1997), any effects of area or isolation on metapopulation dynamics were masked by other patch variables. Factors other than area and isolation yielded high predictive power in several of our occupancy and turnover models. Moreover, more than one aspect of habitat quality was statistically significant (improvement chi-square $p < 0.10$) in 11 of the 15 models. Because we did not perform Bonferroni corrections, we acknowledge the possibility of occasional spurious correlations. But neither area nor isolation was a significant correlate, spurious or otherwise, in any final model of the stepwise logistic-regression analyses. In this system, patch geometry does not appear to be a good predictor of the observed metapopulation dynamics. We

do not claim that patch geometry has no explanatory power, only that area and isolation have demonstrably less explanatory power than other variables.

There are compelling ecological explanations why certain measures of habitat quality, particularly those that were significant in many analyses, were significantly associated with occupancy. For example, disturbance tended to be negatively correlated with occupancy and colonization and positively correlated with extinction. In our study system, livestock grazing was the most widespread form of human-generated disturbance. In the short term, grazing reduces both nectar availability (because livestock consume thistle flowers) and vegetation cover. During the summer, a decrease in plant cover increases exposure of adults and larvae to extreme temperatures and storms. Over longer time spans, grazing can lead to soil compaction, which reduces water infiltration. As patches become more xeric, they are likely to lose larval host plants and to be invaded by non-native grasses. In some analyses, there was an apparent time-lag—often 2 years—in the effect of a disturbance. This lag may be explained simply as a combination of short- and long-term effects on habitat quality. Another possibility is that disturbance in year t reduces, through an array of mechanisms, population size in year $t + 1$. If conditions in year $t + 1$ are unfavorable, the population may go extinct in year $t + 2$.

In 3 of 5 years, some measure of nectar availability (abundance or composition) was positively correlated with occupancy. The positive association between thistles and occupancy probably reflects the fact that nectar is a critical adult resource for many species of butterflies and likely increases female reproductive success in *S. nokomis* (Boggs & Ross 1993; Boggs 1997). In addition, patches with abundant nectar may simultaneously deter emigration and attract dispersing butterflies (Kuussaari et al. 1996; Moilanen & Hanski 1998). Abundance of larval host plants and litter were significantly correlated with occupancy in 1 year each. Although it does not appear that larval host-plant abundance is a limiting resource for *S. nokomis*, females may be less prone to emigrate if they frequently encounter plants suitable for oviposition. Likewise, larvae can spend more time feeding and less time searching for food in patches with abundant host plants. Probability of occupancy decreased as litter increased, perhaps because heavy (as opposed to moderate) cover of litter may impede oviposition.

We also can make reasonable inferences about the association between the significant environmental variables and probability of extinction. First, a relatively high percent cover of vegetation may, like heavy litter cover, limit oviposition. Our results suggest that vegetation cover has a greater impact on *S. nokomis* than vegetation height, possibly because many of the native species of grasses and forbs that grow in mesic, apparently high-quality habitat patches are tall but do not occur at high densities. Second, the decrease in extinction probability

with increasing distance to the nearest extinction site suggests spatially correlated extinctions, which may result from spatially correlated land-management practices and weather patterns. Finally, in one model, probability of extinction decreased when many nearby populations had gone extinct. A possible explanation is that persisting populations received a large number of emigrants from nearby populations in decline. If so, this “rescue effect” (Brown & Kodric-Brown 1977) was the only potential effect of isolation on dynamics detected in our analyses.

Variables correlated with metapopulation dynamics in several models, especially in several multiple-year models, may have greater biological significance than variables that were statistically significant in only one single-year model. For example, populations of *S. nokomis* may be more sensitive to disturbance than to vegetation height. Disturbance in a single year—1995—entered five of the nine models in which disturbance was significant. Demographic data on all resident butterfly species in the Toiyabe Range indicate that climatic conditions were extremely favorable for butterflies in 1995 (Fleishman et al. 1997, 1998). Management practices during years of peak occupancy and abundance in particular may have long-term ramifications if they influence whether potential expansion of the metapopulation will be realized.

Modeling Systems with High Turnover

Our ability to detect correlates of patch occupancy may be inhibited by high rates of turnover. This potential bias is clear in systems with extremely high turnover. If each patch changed state in nearly every time step, any persistent measures of habitat quality would be precluded as correlates of occupancy. The measure of habitat quality most likely to be correlated with occupancy in a system with high turnover is patch isolation. Isolation is not a persistent measure, because it depends on the occupancy of other patches. The occupancy of other patches may be perfectly correlated with the occupancy of a focal patch, regardless of the rate of turnover. Therefore, high-turnover systems may be more likely to reveal the effects of isolation than those of other patch qualities on occupancy. Despite the potential for such bias in the high-turnover *S. nokomis* system, isolation did not enter our occupancy models, providing further evidence that other measures of habitat quality have much greater effects on the dynamics of this metapopulation.

The rate of turnover should have relatively small effects on our ability to detect correlates of extinction or colonization. Each state transition—extinction or colonization—occurs no more than half as frequently as a patch is occupied (and usually much less frequently). Therefore, persistent habitat measures are less likely to be precluded as correlates of turnover. In addition, higher turnover will increase the number of extinction and colonization events

observed, which may actually improve our ability to identify their correlates. Our results provide some support for the prediction that state-transition models may be more appropriate than incidence-function models in high-turnover systems (Sjögren-Gulve & Hanski 2000). The goodness-of-fit p values of our models were >0.5 in only 40% of our occupancy models, compared with 70% of our turnover models (50% of colonization models and 83% of extinction models). State-transition models may be particularly appropriate when it is desirable to identify the potential effects of habitat quality on patch dynamics (Sjögren-Gulve & Ray 1996).

Modeling Occupancy and Turnover through Time

Because local extinctions and colonizations are influenced by environmental and demographic stochasticity, occupancy patterns vary over time (Hanski et al. 1996). Thus, the point at which a snapshot of occupancy is taken can affect parameter estimation and model accuracy. Accordingly, Hanski et al. (1996) and Moilanen (1999) suggest that parameterizing models with data pooled over multiple years should reduce the effect of environmental stochasticity and yield more accurate predictions. Our results suggest, however, that there may be real temporal variation in the determinants of metapopulation dynamics. If so, including multiple years of data in a single model may not be the best strategy for predicting long-term turnover. An alternative strategy might be to apply various single-year models sequentially.

Pooling data over several years can mask the occasional but important influence of certain habitat variables. For example, the relative importance of vegetation cover for *S. nokomis* may depend on the magnitude of extreme climatic events and the grazing-mediated availability of nectar. Spatially correlated environmental stochasticity, whether natural or anthropogenic, may alter extinction rates in particular years, causing sharp changes in metapopulation occupancy that may not be predicted by models that average out the stochastic component of dynamics. For these reasons, we suggest taking a comparative approach to modeling occupancy and turnover, including as many temporal scales of analysis as the data will support.

Rules and Exceptions in Metapopulation Dynamics

When data and resources are limited, researchers and practitioners must rely on dependable first principles that relate available or easily measured data to the biological phenomena of interest (Hanski 1997; Moilanen & Hanski 1998). Although our results may seem paradoxical with respect to the patch-geometry paradigm, we do not question the body of conceptual and empirical research that has established the importance of area and isolation to metapopulation dynamics. Moreover, we

are well aware that few conservation biologists and land managers have the resources with which to conduct long-term assessments of occupancy or turnover, let alone to measure numerous aspects of habitat quality. But the dynamics of *S. nokomis* do demonstrate that systems exist in which occupancy and turnover patterns are not best explained in terms of area and isolation. Instead, extinction and colonization events may be more closely related to multiple aspects of habitat quality that are not static in their relative importance. We hope the current paradigm will expand to emphasize the full complement of environmental variables that may contribute to the dynamics and conservation of metapopulations.

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Annotations from CBI00539.pdf

Page 2

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Page 3

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Watt et al. 1977 — 1979 in Literature Cited.

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