

Range Occupancy and Endangerment: A Test With a Butterfly Community

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ABSTRACT.—Conservation efforts are frequently hampered by uncertainty regarding species' distributions. Range maps as representations of species distributions are known to overestimate the area occupied by the species, with significant implications for the prioritization of conservation efforts among species. We investigate the disparity between extent of occurrence (*i.e.*, “range”) and area of occupancy of a population or species and discuss its implications. Using as a test group a community of subalpine butterflies (Lepidoptera: Papilionoidea), we estimated range occupancy based on three levels of analysis: two field guides with differing mapped resolution of range and microdistribution data collected in the vicinity of the Rocky Mountain Biological Laboratory, near Crested Butte, Gunnison County, Colorado. We conclude butterfly range occupancy across species is low and variable, ranging from 1% to 37% among species present in our sample. A large proportion of species identified as present by range maps in both field guides (70%) were absent from our sample and we present species-specific expert opinion regarding their absence. We demonstrate potential practical and conceptual challenges inherent in the use of range maps to assess endangerment and conservation priority.

INTRODUCTION

It has long been recognized that extent of occurrence (or “range” as it is commonly known and as we use it here) and area of occupancy of a population or species can be quite different (Gaston, 1994). The degree of disparity can obviously have important conservation consequences. Uncertainty regarding species' distributions has been identified as a key barrier to conservation efforts (Millennium Ecosystem Assessment, 2003) and degree of endangerment is not readily determined from field guide distribution maps. Consider, for example, a species with a wide geographic range but actually occupying only a few narrow habitats within that range. If its situation is presented as a range map enclosing all known occurrences, then a person making conservation decisions for this species could overestimate its abundance and thereby overlook conservation needs. Examples are the Edith's and Yellowstone checkerspot butterflies *Euphydryas editha* and *E. gillettii* (Nymphalidae), both of which occur as scattered populations. Populations of *E. editha* are only threatened in parts of the species' range (*e.g.*, regions of California). *Euphydryas gillettii*, on the other hand, is thought to be threatened throughout its range. Yet the range maps of both species in the standard book on North American butterflies (Scott, 1986) unavoidably give the impression that both species occur continuously over areas of tens to hundreds of thousands of square kilometers. Similarly the rare Early Hairstreak butterfly (*Erora laeta*, Lycaenidae) is shown in another excellent field guide (Opler and Krizek, 1984) as occupying a wide swath of the Appalachians, although co-author P. R. Ehrlich and many others familiar with its habits who have collected butterflies in that region have never even seen it. In another case, the Rockslide Alpine *Erebia magdalena* is shown in Scott occupying about a third of Colorado

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when, from experience, we would guess it occupies less than 5%, being confined to scattered talus slopes at high altitude.

There are, of course, a series of important definitional problems associated with the question of how butterfly species "occupy" their ranges. At one extreme, one could select as a parameter to estimate the area that would be "shaded" by individuals of the species at noon on a given day, the purest version of "area of occupancy." At the opposite extreme is a parameter closer to that implicitly used in most field guide maps—the smallest reasonably convex area that encloses all points at which the species has ever been recorded, known as the "range," "gross range" or "extent of occurrence" (Gaston, 1994). More interesting intermediate parameters would be the area "shaded" if the home ranges of all individuals were opaque (*i.e.*, taking movement patterns into consideration) or the extent of potentially available habitat (assuming that over ecological time all of the habitat would be occupied at least sporadically). Our estimate of occupancy is roughly the latter, focusing on habitat availability rather than guessed at home ranges.

Though species range is the more frequently presented and the more readily available of the two distribution metrics, species occupancy is usually the primary concern of conservation studies. Specialists are, of course, often aware of the degree of overestimation in their own groups, but it is ordinarily other biologists, students and amateurs who need and use field guides—and we have often seen the degree to which this misleads about the actual rarity of some organisms and, thus, an underestimation of the seriousness of the extinction problem. Though species endangerment can be obscured by range maps, these hazards are most acute for endangered *populations* and are compounded by the reduced attention given to the problem of population extinction (Hughes *et al.*, 1997).

The unavailability of occupancy data imposes many challenges for conservation. For example, when one is attempting to estimate the amount of population extinction suffered by a given species, differences in historic as opposed to current occupancy can be important. For instance, estimates of population extinction of British butterflies were made too conservative by assuming that presence today in a grid square where the species had occurred historically indicated no population extinctions had occurred in that square when some (but not all) populations actually had disappeared from it (Ehrlich, 1995; Thomas and Abery, 1995). Inability to compare in detail historic area of occupancy of mammal ranges with occupancy of current ranges and thus assuming them identical was almost certainly a conservative factor in estimating levels of continental mammal extinctions (Ceballos and Ehrlich, 2002).

We investigate the disparity between extent of occurrence and area of occupancy of a population or species, sampling a community of Rocky Mountain region subalpine butterflies (Lepidoptera: Papilionoidea). Three levels of analysis contribute to our estimate of range occupancy: two field guides with differing mapped resolution of range and microdistribution data collected with field surveys. Comparing the representation of species across these scales provides approximations of the degree to which the ranges overestimate actual species occupancy.

METHODS

In order to examine the results of different methods of estimating range occupancy, we have selected as a test group a community of subalpine butterflies (Lepidoptera: Papilionoidea) characteristic of open-meadow habitats in the vicinity of the Rocky Mountain Biological Laboratory, near Crested Butte, Gunnison County, Colorado (38°57'N, 106°59'W). The community was defined as all species we found flying in a set of meadows.

At our largest scale, we simply calculated the range area in the Rocky Mountain states (*see below*) given by digitizing the Rocky Mountain distributions (all blacked-in on an outline map of the entire Nearctic realm) of the species of our Colorado test community in Scott's *Butterflies of North America* (1986). At the next most detailed scale we wished to calculate the range area of each species as derived from the standardized county-by-county distribution maps of Ferris and Brown's *Butterflies of the Rocky Mountain States* (1981) (on which there is a single dot in each county of occurrence in an area from the Canadian border to northern New Mexico and Arizona, and from far western Washington and eastern Nevada to western North Dakota and Texas panhandle—roughly 1800 km N-S and 1400 km E-W). To be able to make the comparison legitimate, in the Scott maps we calculated only the area overlying the counties covered in Ferris and Brown (that is, where there was coverage in both books). The choice of Ferris and Brown (FB) for a second scale is simply that it is the best available coverage of butterfly ranges including Gunnison County that is more detailed than that in Scott. The FB presentation gives a more accurate estimate of occupancy, since many counties in which a butterfly is not known to occur are nonetheless necessarily blacked-in on Scott's small maps.

We calculated county-based estimates by including only those counties for which the outline of the county on the FB maps was complete (*i.e.*, some marginal counties were not included in the map in their entirety) and used only those where the presence of the species had been confirmed (dubious records are indicated as such on the maps). The total area of those "complete" counties was the region in Scott's guide that we considered. We summed the planimetric area (treating each county as a plane and not considering the additional area added by topographic relief) of the counties in which the butterfly was found and computed the percentage of the Rocky Mountain region covered in FB that was occupied. Although it may be argued that surface area is a more accurate representation of resources available to butterflies, we assumed the errors in differential surface area to be negligible with respect to the other assumptions of the study. Using relatively mountainous Gunnison county, Colorado as a test case, we concluded that the ratio of surface to planimetric area, calculated with a 1:250,000 scale elevation model was 1.040 and thus did not attempt any correction.

By adding up the areas of the counties with records per the FB maps, we got, under these assumptions, a second, more refined estimate of the range occupied in the Rocky Mountain region—one that took account of numerous "holes" in the distribution which could not be seen in the Scott maps of the same region.

We then determined by field work the actual microdistribution of each of the butterfly species we encountered in a set of meadows in the vicinity of the Rocky Mountain Biological Laboratory (RMBL) at Gothic, Colorado. We used the microdistribution information to make a rough estimate of the proportion of Gunnison county occupied. Then we extrapolated that proportion to all the other counties in the FB region to get an even more refined estimate of what proportion Scott ranges was actually "occupied" on the assumption that the proportion occupied in other counties was about that of Gunnison (obviously a very rough approximation). The procedures used to make this microdistribution-based estimate are now explained in more detail.

Our Gothic sample area, a rectangle 5.6×6.3 km (~ 35 km²), occupied most of USDA-F air photo 24/612040/288-95 (8-14-88). The center of this "Gothic rectangle" was 1.1 km (airline) up Copper Creek Valley from Gothic, and the sides of the rectangle paralleled to those of the photo (roughly N-S and E-W). The overall sample area was very diverse, with valley floor sites being at roughly 3,000 m. It also contained several areas of alpine scree and

tundra at altitudes of some 3700 m. The primary sampling was carried out in 14 meadows that appeared to contain a similarly diverse mix of herbaceous plants, but differed in slope aspect and degree of rock outcrop. The sites were linearly arranged running north from Gothic along the 401 hiking trail on the north slope of East River Valley between altitudes of 2972 m and 3100 m, some 75–100 m above the river. The field work was conducted at the peak of the butterfly flight season from 19 June to 8 August 1998, although some presence-absence data from observations in 1997 (Ricketts *et al.*, 2002) were employed.

DESCRIPTION OF SITES

On the basis of an aerial photo (2 inches:1 mile or 5 cm:1.6 km) and surveys on foot, the land surface was classified into seven land cover types. Within representative sites of each habitat, 2100 m² sampling plots were established.

- a) Diverse Meadow. Composed of a mix of herbaceous plant species, the meadows appeared similarly diverse but varied in the amount of rock cover. Fourteen sites were linearly arranged along the East River valley (running north of Gothic) for 3 km. The sites ranged in elevation from 2972 m to 3100 m.
- b) Meadow dominated by *Veratrum tenuipetalum* (corn husk lily; false hellebore). Three sites were selected in the East River Valley.
- c) Meadow dominated by *Salix* spp. (willows). Three sites were selected, two in the East River Valley and one in the Adjacent Copper Creek Valley.
- d) Talus slopes. Characterized by areas of broken rock, this habitat type supported very little plant biomass. Three sites were selected: two in the East River Valley and one in the copper Creek Valley. Although the talus was sampled independently, we pooled the talus data with the tundra data in our analysis, as described below.
- e) Tundra. This above-treeline habitat generally occurred at 3600 m and higher and was composed of a diverse array of short herbaceous plants. Given constraints of access, weather and the short duration of the flight season, these sites were surveyed briefly during our sample period. Although the tundra was sampled independently, we pooled the tundra data with the talus data in our analysis, as described below.
- f) Aspen (*Populus tremuloides*) woodlands. This habitat was surveyed in the 1997 flight season by Ricketts and, due to the lack of butterflies, was not surveyed during this investigation.
- g) Spruce (*Picea engelmannii*) woodlands. Again this habitat was surveyed in the 1997 flight season by Ricketts and was not surveyed during this investigation.

The proportion of land cover types was determined first by ground-truthing—assigning areas on the air photo to the different habitats—and then by cutting out the areas of habitat from the physical photograph and weighing them to produce a proportion of cover for each habitat type. Ground-truthing proved prohibitively difficult in the most remote areas of our Gothic rectangle, specifically the tundra and talus land-cover types. To avoid confusing them, we pooled the tundra and talus air-photo regions, which may slightly inflate occupancy for those species which were recorded in one or the other of those two land-cover types.

SAMPLING PROTOCOL

We did not attempt to sample evenly over all land cover types. Because of its known butterfly richness, the diverse-meadow habitat was the most intensively sampled. The sampling plot at each diverse-meadow site was surveyed for 316–323 person-minutes spread evenly over 23 surveys throughout a fifty-day period. The *Veratrum*-dominated, *Salix*-

dominated and talus-dominated land cover types were known to support a limited butterfly richness and were sampled less intensively, for a minimum of 120 person-minutes spread over 6 surveys throughout a 41 d period. Due to its remote location and short warm season in which butterfly collecting is possible, the tundra was also sampled less intensively; each site was surveyed for 60 person-minutes in one survey. The aspen and spruce woodlands were sampled in the 1997 flight season. Sampling effort was distributed equally across sites with respect to time of day, light intensity, temperature and wind speed. Different numbers of sites and sampling intensity across land cover types will introduce differential variance across sites, but this does not introduce relevant bias given our analysis. The advantage of more intensively sampling those land cover types with the greater butterfly abundance is clear.

In each sampling period, two investigators paced through the entire plot and attempted to capture all butterflies found. Captured specimens were identified to species using (Scott, 1986). The observation of uncaptured individuals that could be identified to genus or species was also recorded; this was a relatively rare event, confined mostly to lycaenids that were observed sitting and then were missed with the net or *Papilio zelicaon*, which is unmistakable when speeding across a plot.

DATA ANALYSIS

Table 1 shows the procedure for calculating occupancy at the microdistribution level for a few representative species in our sample, as explained in the table legend.

To see how we calculated range occupancy, consider the first species in Table 2, *Erebia epipsodia*. The first column is the "Scott area," the area computed by digitizing the Scott map of the *E. epipsodia* distribution where it overlaps the FB map, 777,118 km². The second column sums the total area of the counties in FB in which *E. epipsodia* has been recorded, 660,732 km². The third column divides the FB area by the Scott area to give the proportion of the Scott range that *E. epipsodia* actually "filled" by the Ferris/Brown criterion, 0.85. The fourth column is the estimate of the proportion of the land area in our Gothic rectangle over which *E. epipsodia* flies (*i.e.*, the last column in Table 1), in this case 0.30. And, finally, the fifth column is the extrapolation to the proportion of the entire Scott range actually occupied by *E. epipsodia*, 0.26, on the assumption that all "occupied" counties harbor the same proportional microdistribution of this species. That is an extreme and doubtless incorrect assumption—there are clearly some counties that would have proportionately more habitat for each species and others with proportionately less. There is no sizeable group of organisms where habitat availability is known, for the Rocky Mountains or any comparable area to a precision that would permit a country by county judgment of availability (indeed our study is one of the first to attempt this at any scale), and no prospect that the enormous effort that would be required will be mounted, even for intensely-studied groups such as British butterflies or birds. Therefore, our assumption is necessary, and we have no reason to believe there is any particular direction in the biases.

The last element in our study was an examination of how our test Gothic community sampling and the county sampling (FB) related to the overall impression of the butterfly distributions as represented in Scott's book, summarized in Table 3.

Butterfly nomenclature is a continually evolving mess, due to evolution of knowledge of the group. In all cases we have followed that in Scott, which is generally sensible for communication, except for *Pieris mcduunnoughi*, which is very distinct from the European *P. napi*, and *Colias eriphyle*, which in the past has been confused with *C. philodice*, actually a derivative of *C. eurytheme* (Ward Watt, pers. comm.). In one case, that of *Cercyonis sthenele / oetus* we have omitted the organism from our analysis because of uncertainty over which

TABLE 1.—This table presents the procedure for calculating microdistributional occupancy for a representative selection of species across all habitat types. The first column shows the map-derived proportion of meadow area to total land area within our Gothic rectangle. The second column shows the proportion of sampled meadows in which we encountered that species in our field season. Columns 3 through 8 repeat this analysis for the other habitat types (spruce- and aspen-dominated areas had zero occupancy and therefore did not contribute to the last column). The three talus and three tundra sites are pooled as explained in our Methods. Lastly, column 9 sums the area-occupancy products of each pair of columns to generate an overall proportion of occupancy for the entire Gothic rectangle

	Proportion of meadow in landscape	Proportion of meadows occupied ($n = 14$)	Proportion of willow in landscape	Proportion of willow occupied ($n = 3$)	Proportion of talus/tundra in landscape	Proportion of talus/tundra occupied ($n = 3/3$)	Proportion of veratrum in landscape	Proportion of veratrum occupied ($n = 3$)	Proportion of Gothic rectangle occupied
<i>Erebia epipsodia</i>	0.42	0.71	0.02	0.02	0.19	0.19	0.01	0.01	0.30
<i>Oeneis chryxus</i>	0.42	0.57	0.02	0.33	0.19	0.33	0.01	0.01	0.31
<i>Vanessa atalanta</i>	0.42	0.29	0.02	0.02	0.19	0.17	0.01	0.01	0.15
<i>Nathalis iole</i>	0.42	0.07	0.02	0.02	0.19	0.19	0.01	0.01	0.03
<i>Pieris medannoughi</i> ("napi")	0.42	1.00	0.02	0.67	0.19	0.33	0.01	0.67	0.51

TABLE 2.—This table displays the results of extent of occurrence or area of occupancy at each of the three scales in our analysis and the final occupancy figure derived from these values (in the last column)

	Scott area (km ²)	County area (km ²)	County area/ Scott area	Proportion of Gothic rectangle occupied	Occupancy of Scott range
<i>Erebia epipsodia</i>	777,000	660,732	0.850	0.30	0.26
<i>Coenonympha tullia</i>	1,607,000	1,267,585	0.789	0.30	0.24
<i>Oeneis chryxus</i>	848,000	697,242	0.822	0.31	0.26
<i>Chlosyne palla</i>	1,607,000	569,432	0.354	0.36	0.13
<i>Euptoieta claudia</i>	1,806,000	758,200	0.420	0.36	0.15
<i>Nymphalis milberti</i>	1,715,000	1,077,981	0.629	0.06	0.04
<i>Phyciodes campestris</i>	1,543,000	1,148,999	0.745	0.12	0.09
<i>Polygonia zephyrus</i>	1,275,000	966,519	0.758	0.15	0.12
<i>Speyeria atlantis</i>	1,385,000	1,016,597	0.734	0.15	0.11
<i>Speyeria mormonia</i>	1,194,000	918,819	0.769	0.49	0.37
<i>Vanessa atalanta</i>	1,811,000	966,393	0.534	0.15	0.08
<i>Vanessa cardui</i>	1,812,000	1,236,554	0.683	0.10	0.07
<i>Agriades glandon</i>	901,000	710,971	0.789	0.33	0.26
<i>Everes amyntula</i>	1,269,000	880,035	0.694	0.09	0.06
<i>Glaucopsyche lygdamus</i>	1,597,000	1,083,284	0.678	0.06	0.04
<i>Hemiargus isola</i>	1,228,000	497,291	0.405	0.03	0.01
<i>Lycaena heteronea</i>	1,158,000	849,980	0.734	0.39	0.29
<i>Lycaena nivalis</i>	808,000	442,879	0.548	0.36	0.20
<i>Plebejus acmon</i>	1,777,000	888,466	0.500	0.18	0.09
<i>Plebejus melissa</i>	1,809,000	1,318,645	0.729	0.15	0.11
<i>Plebejus saepiolus</i>	1,494,000	1,086,376	0.727	0.15	0.11
<i>Colias alexandra</i>	1,552,000	1,037,218	0.668	0.40	0.27
<i>Colias eriphyle</i> ("philodice")	1,809,000	1,406,397	0.778	0.27	0.21
<i>Colias scudderii</i>	454,000	200,613	0.442	0.03	0.01
<i>Euchloe ausonides</i>	1,532,000	1,011,888	0.661	0.36	0.24
<i>Nathalis iole</i>	1,580,000	544,459	0.345	0.03	0.01
<i>Pieris mcdunnoughi</i> ("napi")	1,311,000	874,857	0.667	0.51	0.34
<i>Pieris occidentalis</i>	1,400,000	930,411	0.665	0.52	0.34
<i>Pieris protodice</i>	1,768,000	1,104,199	0.625	0.37	0.23
<i>Papilio eurymedon</i>	1,093,000	608,220	0.557	0.09	0.05
<i>Papilio zelicaon</i>	1,578,000	892,694	0.566	0.19	0.10

entity is considered in each source (and their relationship to each other). Comments on the ecology of different species are based on Scott; Ferris and Brown; (Brown, Eff and Rotger, 1957) and personal observations of Carol Boggs, Gretchen Daily, Paul Ehrlich, Taylor Ricketts and Ward Watt (~125 person/seasons in the Gothic sample area).

RESULTS

Our basic results on percentage of area occupied by the butterflies are given in Table 2. The average occupancy (column 5) was 16% and no species had much more than a one-third calculated occupancy of their continental range. The range of values is also of interest, with one species (*Colias scudderii*) occupying only 1% of its range.

Table 3 lists the species shown to be in Gunnison County by the Scott continental maps (column 1), those shown to be in Gunnison County by Ferris and Brown (column 2) and those that we found in our Gothic rectangle (column 3). The final column provides our assessment of why the 83 species otherwise shown to be in Gunnison County were absent

TABLE 3.—This table lists the representation of the butterfly species of Scott's Butterflies of North America (1986) shown to overlap the distribution area of Ferris and Brown's Butterflies of the Rocky Mountain States (1980), their representation in FB maps, and their recorded presence in our Gothic-rectangle field sample. In the last column we provide informed speculation on why the species shown in Scott to be in Gunnison County were absent from our sample

Species	Scott	Ferris	Sample	Note
<i>Papilio machaon</i>	x			H (too high)
<i>Papilio zelicaon</i>	x	x	x	
<i>Papilio indra</i>	x			H (too high)
<i>Papilio rutulus</i>	x	x	x	
<i>Papilio eurymedon</i>	x	x	x	
<i>Papilio multicaudata</i>	x	x		H (too high)
<i>Parnassius phoebus</i>	x	x	x	
<i>Colias alexandra</i>	x	x	x	
<i>Colias meadii</i>	x	x	x	
<i>Colias eurytheme</i>	x	x		V
<i>Colias eriphyle</i> ("philodice")	x	x	x	
<i>Colias scudderii</i>	x	x	x	
<i>Colias cesonia</i>	x	x		V
<i>Phoebis sennae</i>	x	x		V
<i>Eurema nicippe</i>	x	x		V
<i>Eurema mexicana</i>	x	x		V
<i>Eurema lisa</i>	x			V
<i>Nathalis iole</i>	x	x	x	V
<i>Anthocharis sara</i>	x	x		P/S (earlier)
<i>Euchloe ausonides</i>	x	x	x	
<i>Euchloe hyantis</i>	x	x		H/P (too high, earlier)
<i>Pieris rapae</i>	x	x		S
<i>Pieris mcdunmoughi</i> ("napi")	x	x	x	
<i>Pieris chlorodice</i> (<i>beckerii</i>)	x	x		H
<i>Pieris protodice</i>	x	x	x	
<i>Pieris callidice</i> (<i>occidentalis</i>)	x	x	x	
<i>Pieris sisymbrii</i>	x	x		H/P (too high, earlier)
<i>Neophasia menapia</i>	x	x		H (pine)
<i>Danaus plexippus</i>	x	x		V
<i>Danaus gilippus</i>	x	x		V
<i>Cyllopsis pertepida</i>	x	x		H (too high)
<i>Coenonympha tullia</i>	x	x	x	
<i>Cercyonis pegala</i>	x	x		H (too high)
<i>Cercyonis sthenele</i>	x	x		?
<i>Cercyonis oetus</i>	x	x	x	
<i>Erebia magdalena</i>	x	x		S
<i>Erebia epipsodea</i>	x	x	x	
<i>Erebia callias</i>	x	x		S
<i>Neominois ridingsii</i>	x	x		H (too moist)
<i>Oeneis chryxus</i>	x	x	x	
<i>Oeneis uhleri</i>	x	x		S
<i>Oeneis jutta</i>	x	x		H
<i>Oeneis melissa</i>	x	x		S
<i>Oeneis polixenes</i>	x	x		S
<i>Oeneis bore</i>	x	x		S
<i>Limenitis archippus</i>	x			V/H (too high)

TABLE 3.—Continued

Species	Scott	Ferris	Sample	Note
<i>Limenitis weidemeyerii</i>	x	x		S
<i>Vanessa atalanta</i>	x	x	x	
<i>Vanessa cardui</i>	x	x	x	
<i>Vanessa virginiensis</i>	x	x		S
<i>Vanessa anabella</i>	x	x		S/V
<i>Polygonia satyrus</i>	x	x		S
<i>Polygonia gracilis</i>	x	x	x	
<i>Polygonia faunus</i>	x	x		S
<i>Nymphalis milberti</i>	x	x	x	
<i>Nymphalis antiopa</i>	x	x		S
<i>Euphydryas editha</i>	x	x		S
<i>Euphydryas anicia</i>	x	x	x	
<i>Poladyras arachne</i>	x	x		S
<i>Chlosyne gorgone</i>	x	x		H (too high?)/S
<i>Chlosyne nycteis</i>	x	x		H (too high?)/S
<i>Chlosyne palla</i>	x	x	x	
<i>Chlosyne gabbii</i>	x	x		H (too high)
<i>Phyciodes pallida</i>	x	x		H (too high)
<i>Phyciodes morpheus</i>	x	x		S (too high?)
<i>Phyciodes campestris</i>	x	x	x	
<i>Boloria eunomia</i>	x	x		S (too low?)
<i>Boloria selene</i>	x	x		S
<i>Boloria titania</i>	x	x		S
<i>Boloria bellona</i>	x	x		S
<i>Boloria frigga</i>	x	x		S
<i>Boloria freija</i>	x	x		S
<i>Speyeria aphrodite</i>	x	x		H
<i>Speyeria cybele</i>	x	x		H
<i>Speyeria mormonia</i>	x	x	x	
<i>Speyeria callippe</i>	x	x		extinct?
<i>Speyeria atlantis</i>	x	x	x	
<i>Speyeria zerene</i>	x	x		H
<i>Speyeria coronis</i>	x	x		H
<i>Speyeria edwardsii</i>	x	x		H
<i>Euptoieta claudia</i>	x	x	x	
<i>Apodemia mormo</i>	x	x		H (too high)
<i>Hypaurotis chrysalis</i>	x	x		H (too high, no oaks)
<i>Harknclenus titus</i>	x	x		S
<i>Satyrium californica</i>	x	x		H (too high)
<i>Satyrium sylvinus</i>	x	x		H (too high)
<i>Satyrium liparops</i>	x	x		H (too high)
<i>Satyrium calanus</i>	x	x		H (too high)
<i>Satyrium saepium</i>	x	x		H (too high)
<i>Satyrium behrii</i>	x	x		S
<i>Callophrys eryphon</i>	x	x		H (no pines)
<i>Callophrys polios</i>	x			H (Too high)
<i>Callophrys augustus</i>	x	x		H (no pines)
<i>Callophrys gryneus (siva)</i>	x	x		H (no junipers)
<i>Callophrys spinetorum</i>	x	x		S
<i>Callophrys affinus</i>	x	x		H (too high)

TABLE 3.—Continued

Species	Scott	Ferris	Sample	Note
<i>Callophrys sheridani</i>	x	x		H (too high)
<i>Strymon melinus</i>	x			H/P?
<i>Lycaena cupreus</i>	x	x		S (tundra)
<i>Lycaena nivalis</i>	x	x	x	
<i>Lycaena helloides (+dorcias)</i>	x			S
<i>Lycaena heteronea</i>	x	x	x	
<i>Lycaena rubidus</i>	x	x		S
<i>Lycaena arota</i>	x	x		H (too high)
<i>Everes amyntula</i>	x	x	x	
<i>Celastrina argiolus</i>	x	x		P (flies early)
<i>Glaucopsyche lygdamus</i>	x	x	x	
<i>Glaucopsyche piasus</i>	x	x		S
<i>Euphilotes battoides</i>	x			H (too wet?)
<i>Euphilotes enoptes</i>	x	x		H (too wet?)
<i>Euphilotes spaldingi</i>	x	x		H (too high, dry)
<i>Plebejus glandon</i>	x	x	x	
<i>Plebejus idas</i>	x	x		H (too low?)
("argyrognumen")				
<i>Plebejus melissa</i>	x	x	x	
<i>Plebejus saepiolus</i>	x	x	x	
<i>Plebejus icarioides</i>	x	x		S
<i>Plebejus shasta</i>	x	x		H (too low)
<i>Plebejus acmon</i>	x	x	x	
<i>Hemiargus isola</i>	x	x	x	
Column Totals	119	111	36	

P = phenology miss (probably present earlier in spring)

S = sampling error (has been seen in 35 km quadrat or expected to be found in it)

H = habitat not in quadrat

V = vagrant or migrant

from our community sample—based on information in (Brown *et al.*, 1957) and our experience at RMBL. While there are some problems of nomenclature and sampling inherent in this list, the basic conclusions are robust. Both Scott and FB range maps vastly overestimate the occupancy of the butterfly species studied.

Three species in our microdistribution sample were encountered exclusively in the tundra land-cover type (*Parnassius phoebes*, *Euphydryas anicia* and *Colias meadii*). Since the tundra type is contingent on elevation in the Rocky Mountain region, we expect its percent cover to be most variable across the counties included in FB. We therefore excluded these species from the analysis in Table 2, since an occupancy percentage derived from our data would be highly error-prone.

Of the species indicated as present in the county containing the Gothic sample area, 83, or 70%, were not found in our survey. These results also provide an estimate of the proportion of species for which our sample area was unoccupied habitat during our sampling period. Our notes in column 4 of Table 3 provide an expert explanation of absence from our sample. From these assessments, it is apparent that some 38 species were not sampled despite potential occupancy of the sample rectangle at some point in the year (*i.e.*, have sampling (S) or phenology (P) as part of their explanation in Table 3). That number includes the possibly locally extinct *Speyeria callippe*, but not unsampled vagrants. Combining

these species with recorded species, we found 71, or approximately 62%, of the species indicated by Scott as present in his range maps of our sample area are expected to be found in our sample region. Only 51% of these actual and assumed occupants were found in our sample. That is, about half of the species shown to potentially traverse the sampled sites were found in them over the duration of our observations.

Our analysis did not reveal a significant relationship ($R^2 = 0.027$) between (non-zero) percent occupancy and extent of occurrence (per Scott range maps overlying the FB coverage). In other words species that “fill” their ranges densely don’t necessarily have very large ranges.

DISCUSSION

There were many Gunnison County species we did not find in our surveys. That more intensive sampling would have turned up one or more of these species, or that a population explosion in another year might have made numerous individuals on “missing” species present, is undeniable. We expect the microdistribution of individual species to have some variation over time as demographic units expand and send dispersers to “empty” meadows or other habitats or undergo extinctions. But to the extent that the overall occupancy pattern of the summer of 1998 is representative, the general pattern of percentage occupancy may be expected not to vary much in the absence of large-scale climatic or other change (and casual observation by one of us, P. E. Ehrlich, over 40 y indicates that it has not). County occupancy may also show some variation, especially in counties with low or fluctuating local reproduction (population sinks).

Several points are clear. Not surprisingly, extent of occurrence (range) almost always overestimates area of occupancy. Nonetheless, macroecological studies will continue to deal mostly with range, for logistical reasons if for no other. And for many applications, such as comparing the latitudinal distributions of, say, terrestrial mammals, or comparing the average ranges of different subfamilies of butterflies, the overestimate will be of little or no consequence. What this study and some others indicate is that in some, and perhaps most, cases range (extent of occurrence) maps give a very false impression of both the areas of occupancy and thus the implicit abundances of species (Cowley *et al.*, 1999).

While the degree (*i.e.*, magnitude) of occupancy was surprisingly small among the species in our sample, equally of interest is the distribution of these values across species. As with much of our analysis, the details are likely sensitive to our extrapolation of habitat variables, but species present in our sample were determined to occupy from 1% to 34% of their Scott range. This spread of values can undermine conservation initiatives that employ species range maps for prioritization—two species with equivalent range areas may have a 30-fold difference in area of occupancy (Table 2). For example, *Pieris mcdunnoughi* (“napi”) has the highest percentage occupancy, likely because its frequent occurrence in shaded habitats and along wooded stream sides (where some of its food plants grow) leads it to wander in areas not frequented by most species. Its altitudinal range also extends higher than most of the meadow butterflies censused, and individuals are frequently seen traversing wooded areas. *Speyeria mormonia*, in contrast, would seem to claim second place because of its large population size and expansive home ranges. At the other extreme, neither *Nathalis iole* and *Hemiargus isola* appear to overwinter in Colorado, and at least the former may be less common in our samples than it would have been if we had extended our sampling to the middle of Sep., since that species presumably invades the area each season from the south and east. *Colias scudderii* is generally considered scarce by collectors, and its low occupancy is not surprising; *Speyeria callippe* has not been observed in the areas of Colorado near our

sample since before 1991 and, as suggested above, now may be regionally extinct. *Nymphalis milberti*, which is extremely widespread in the Nearctic (and, indeed, would be considered by some circumpolar) seems a first glance to have an unexpectedly low occupancy — one might expect its occupancy to be closer to that of *Polygonia faunus*. But in the Gothic area it tends to “hilltop” on the mountains and be commoner at high altitude during the study period than in the intensively sampled meadows.

Glaucopteryx lygdamus also seems to have a lower than expected occupancy, perhaps a function of its having an earlier and shorter flight season than related species such as *Agriades glandon*. The failure to find *Plebejus icarioides* is even more striking at first glance. It normally seems one of the most abundant lycaenids in the Gothic area, and failure to record it emphasizes the way sampling problems can afflict estimates of range occupancy at a fine scale. The lycaenids are most easily observed as males in “muddle puddle clubs”—sipping water at moist spots in roads. In the meadows themselves they are more difficult to see and often impossible to identify to species on the wing. It is noteworthy that (Ricketts *et al.*, 2002) also did not record *P. icarioides* although they sampled many of the same meadow sites as we did. *P. icarioides* has *Lupinus caudatus* as its primary larval food plant in the area and it tends to be associated with that plant on drier slopes, not with the abundant meadow nectar sources (Sharp *et al.*, 1974). Thus, not only are there large areas within range maps that are devoid of the species mapped, but also even rather intensive community sampling which does not target a given species can easily lead to false negatives in the area sampled. We were essentially attempting to “ground truth” ranges and yet failed to record species we knew from prior, subsequent, and simultaneous experience to be present (*e.g.*, *Plebejus icarioides* was observed in the Gothic area in 1998, but not recorded in the surveys).

The results of this analysis emphasize the importance of carefully considering how range maps are used and how they are perceived. Interspecific comparison of extent of occupancy is only valid when combined with other data — for example, land-use change is expected to have different effects on a sparse, wide-ranging species and a dense, localized species (Warren *et al.*, 2001). For most conservation applications, area of occupancy and density are more desirable data than range. The value of extent of occurrence data *per se* is unclear and problematic when inadvertently conflated with area of occupancy.

The determination of range by the standard method fails to represent occupancy through two inevitable insensitivities. First, it does not employ habitat data to ensure the requisite abiotic (*e.g.*, temperature) and biotic (*e.g.*, hostplant availability) factors for a species' presence—which constitutes an overestimation of the potential range of the species. Second, it usually includes those habitable patches which are empty in the dynamic equilibrium of a metapopulation or wholly outside the dispersal range of extant populations, which compounds the overestimation inherent in considering extent of occurrence. While subjecting the range to a filtering process involving habitat variables might improve its representation of area of occupancy, hostplant availability, species dynamics and sampling problems will confound attempts to accurately determine potential ranges (where the organism could manage to maintain populations) and realized ranges (where it actually does maintain them) despite, in some cases, ground-truthing or complex modeling.

The difficulty of estimating suitability is often underestimated, confounding indirect methods for estimation of occupancy. (Fleishman *et al.*, 2003) describe the complicated tradeoffs and pitfalls that occur with a range of predictive occurrence models for butterflies. These methodological challenges are exacerbated by populations' capriciousness. For example, in the Gothic study area large patches of habitat appeared suitable for

Euphydryas gillettii, a checkerspot butterfly whose natural range is in the northern Rocky Mountains of the United States and southern Canada. A member of a European species group, the butterfly was not found south of the Red Desert gap in the Wyoming Rockies. In 1977 an experimental introduction was attempted at Gothic (Holdren and Ehrlich, 1981). A population persisted there at small size until the early 21st Century and then underwent a local population explosion through 2005 it was still not clear whether the habitat was fully suitable, but recent data suggest that it is (Boggs *et al.*, 2006).

Subjecting the data for the 83 species recorded in Gunnison county, but absent from our survey, to the analysis performed in Table 2 would generate a zero-percent occupancy of their range. The absence of these species from our sample (and the absence of some from the Ferris sample) reinforces the conclusion that range maps may provide a picture of occupancy that greatly overestimates what organisms are likely to be present (or encountered) in a given area. Although our sample size of one area allows little capacity for inference, the absence of two-thirds of the indicated species from an area greater than 30 km² (given our sampling effort) is compelling.

The expectation of species occupancy is also affected by macroecological patterns. On a continental scale of analysis, the coasts provide absolute boundaries to species' ranges, producing intrinsic macroecological patterns (Brown, 1995). Since a convex boundary enclosing observational records cannot contain irregular (*i.e.*, fluctuating or vagrant) records beyond the coasts, a point that is more coastal is less likely to be marginally or debatably within the extent-of-occurrence boundary. Therefore, our rough approximation of 38% for Rocky Mountain species expected to be absent from an area of our sample size would be an upper bound, expected to decline near continental margins. It should be noted that few of the species in the Gunnison County sample (FB) are at the edges of their range at the Gothic rectangle, although some do reach a western limit where the high Rockies end ~30 km west of the rectangle.

Our analysis is sensitive to the number of steps in scale that is used. If we had not employed the Ferris and Brown data, occupancy would have been incorrectly assumed to be much higher because we would have necessarily extrapolated to the entire Scott range instead of only to the area of the counties known to be occupied. The diminishing returns of attempting to incorporate mapped distributions at additional scales suggest that our analysis suffices as an approximation of area of occupancy. Verification is hampered by the lack of data at intermediate scales and our results could be somewhat different if we had used different habitat classifications.

In creating range maps, the accuracy of the map is often judged by the quantity of included observations, that is, a map is considered faulty if compiled from too few records. A larger set of observations can be obtained by using records extending further into the past. Thereby, a rapid contraction of a species' potential or realized range could be obscured by the use of an otherwise "more accurate" map. This tradeoff imposes subtle, rarely conveyed methodological biases in the creation of range maps for dynamic populations—bearing on their use in assessing extent and occupancy. Other factors being equal, a map with a briefer sampling interval will produce a smaller overestimation of species occupancy.

Drawing a range map based on presence data in the manner of Scott also requires (often implicit) consideration of sampling effort. Areas without sightings are either true absences or simply areas without records. There will be an interaction between the interpretation of areas without observations and the intuitive imposition of convexity and integrity (*i.e.*, connectedness). This tradeoff introduces an additional methodological degree of freedom into the range-drawing process.

One final point is the role of species' relative mobilities in facilitating observations. An individual of a vagile species such as *Speyeria mormonia* will be observed in more sites, leading (other factors being equal) to a larger contribution to the species' occupancy as we define it. Species also have differing tendencies to traverse non-resource-providing, conduit areas, which will affect their landscape occupancy in our analysis (Ricketts, 2001). For the purposes of conservation, the operative criterion is the existence of viable populations rather than the presence of vagrant individuals. The challenge of compensating for species mobility in occupancy determination is a conceptual rather than practical one. Should the definition of occupancy be contingent on mobility? In our study, the inclusion of vagrant individuals from distant populations could serve to inflate our analysis. Therefore, our estimate of percent occupancy is conservative and might be made considerably lower by removing vagrants from the sample.

Our primary conclusion is that butterfly range occupancy across species is low and variable. Furthermore, a large proportion of species identified as present by range maps often will likely not be observed at a site with prolonged and extensive sampling. Even filtering these species by habitat requirements leaves a large proportion of species with unoccupied or rarely-occupied areas that appear to be suitable habitat. We also demonstrate potential practical and conceptual challenges inherent in the use of range maps to assess endangerment.

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