Great Basin Naturalist 59(1), ©1999, pp. 50–62

BUTTERFLIES OF THE TOQUIMA RANGE, NEVADA: DISTRIBUTION, NATURAL HISTORY, AND COMPARISON TO THE TOIYABE RANGE

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ABSTRACT.—Studies of Great Basin faunas can provide information for landscape-level adaptive management by federal agencies and shed light on potential effects of climate change in continental interior landscapes. To provide such information, we characterized the butterfly fauna of the Toquima Range, a mountain range in the heart of the Great Basin with topography typical of the region. We also compared the butterfly fauna of the Toquima Range to that of the adjacent Toiyabe Range, which is more topographically complex and species rich but less representative of the Great Basin on the whole. We explicitly addressed the effects of area and water availability on butterfly species richness. Butterfly species presence data were compiled for 14 canyons and 1 peak in the Toquima Range. Data from 11 canyons that we inventoried systematically were amenable to statistical analysis. Eighty butterfly species (59 residents) have been recorded from the Toquima Range since 1935. By comparison, 99 species have been recorded from the Toiyabe Range. Mean canyon-level butterfly species richness was significantly lower in the Toquima Range than in the Toiyabe Range. This difference cannot be explained by differences in canyon size between the mountain ranges. Within the Toquima Range water availability seems to have a dominant effect on butterfly species richness. Between mountain ranges species richness is influenced by interactions among area, moisture, and topography. These data should assist managers in developing guidelines for conservation planning in the Great Basin.

Key words: Toquima Range, Toiyabe Range, butterflies, species richness, riparian habitat, conservation, ecosystem management.

One of Earth's forlorn landscapes, the high desert is bitterly cold in winter, stifling hot in summer, and dry. Situated in an effective rain shadow, the Great Basin encompasses nearly 430,000 km^2 of internal drainage extending from the east slope of the Sierra Nevada and southern Cascades to the west, the west slope of the Wasatch Range to the east, the Columbia River to the north, and the Colorado River to the south (Grayson 1993). At the austere center of the Great Basin lies the Toquima Range. At first glance the Toquima Range is unremarkable. It is neither particularly extensive in area nor, for most of its crest, especially high in elevation. Riparian canyons, known in arid regions for their concentrations of plants and wildlife (Kauffman and Krueger 1984, Armour et al. 1991, Dawson 1992, Dobkin et al. 1998), are the exception rather than the rule in the Toquima. Prominent topographic features, including lakes and pronounced peaks that attract tourists and backcountry enthusiasts, are largely absent from the range. Yet the geography, biology, anthropological history, and even politics of the Toquima Range encapsulate the Great Basin. We were drawn to study the butterfly fauna of the Toquima Range not only because the range is the literal and figurative heartland of the Great Basin, but also to compare it with that of the Toiyabe Range, a neighboring range with subalpine peaks and incised canyons that are far more spectacular, but considerably less typical of the Great Basin as a whole (Trimble 1989, Grayson 1993, Fleishman et al. 1997).

Few studies of Great Basin butterflies have concentrated on the region's center. Compared to faunas present in the Sierra Nevada and Rocky Mountains, central Great Basin butterflies as a group are neither notably rich in species nor in endemic taxa (Wilcox et al. 1986, Austin and Murphy 1987) and have attracted relatively few amateur and professional biologists. However, the region provides an excellent template for research on the potential effects of climate change on butterfly

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and other animal and plant communities in temperate continental interior landscapes (e.g., McDonald and Brown 1992, Murphy and Weiss 1992, Fleishman et al. 1998). Moreover, federal and state agencies responsible for maintaining viable populations of animals and plants in the Great Basin are eager for data on community composition and broad-scale ecological patterns; these data are needed to implement effective landscape-level and adaptive management in the region (Stohlgren et al. 1995, Czech and Krausman 1997, Lambeck 1997, Heikkinen 1998, Simberloff 1998).

The definitive faunal study of central Great Basin butterflies to date (Fleishman et al. 1997) was conducted in the Toiyabe Range, a scant 10 km to the west of the Toquima Range. Also centrally located, the Toiyabe Range is unusually large (3126 km^2; see Biological Resources Research Center [BRRC] 1997), mesic, and biologically diverse relative to many Great Basin ranges (Trimble 1989, Grayson 1993). With a crest that exceeds 3000 m for 40% of its length, it accumulates a substantial snowpack that replenishes streams and delays senescence of riparian and upland vegetation. Biological patterns in a more "typical" Great Basin mountain range, such as the Toquima, arguably may have greater generality. In addition, because the Toquima and Toiyabe ranges have similar biogeographic and management histories (Murphy and Wilcox 1986, Wilcox et al. 1986, Austin and Murphy 1987), our research allowed us to address the effects of area and water availability on butterfly species richness in arid regions.

STUDY AREA

The Toquima Range is located in Lander and Nye counties, Nevada, less than 10 km from the geographic center of the state (Grayson 1993, BRRC 1997; Fig. 1). The 125-km-long, 1750-km^2 range is roughly linear and, typical of most Great Basin mountains, oriented north–south. Roughly 90% of its crest lies at about 2700 m, approximately 500–600 m above Big Smoky Valley to the west and Monitor Valley to the east. A 13-km stretch of the Mount Jefferson ridgeline, with 3 summits above 3300 m, rises above the rest of the Toquima crest (Grayson 1993). Compared to much of the Toquima Range, the local climate of Mount Jefferson is atypically cold (up to 10°C cooler near the top than at the base of the peak on a clear day) and mesic (Trimble 1989, Hidy and Klieforth 1990, E. Fleishman personal observation). Numerous canyons cut the east and west slopes of the Toquima Range. A few of these canyons have perpetually flowing streams, and several have seeps or springs, but most are dry. Topography of individual canyons varies widely.

With increasing elevation in the Toquima Range, dominant vegetation shifts from sagebrush (*Artemisia tridentata* ssp.) to piñon-juniper (*Pinus monophylla*, *Juniperus osteosperma*) woodland to low brush (Tueller and Eckert 1987). A limber pine (*Pinus flexilis*) krummholz grows at timberline, and the summit slopes of Mount Jefferson are inhabited by a depauperate alpine flora (Trimble 1989, Grayson 1993). Patches of mountain mahogany (*Cercocarpus ledifolius*) occur within and above the piñon-juniper zone, and aspen (*Populus tremuloides*) grows in riparian canyons and around seeps on exposed slopes. Canyons with permanent or ephemeral surface water often have willow (*Salix* spp.), rose (*Rosa woodsii*), nettle (*Urtica dioica*), and an understory composed of various grasses and forbs. Two plants considered sensitive by federal agencies, Toquima milkvetch (*Astragalus toquimanus*) and Toiyabe buckwheat (*Eriogonum esmaraldensis toiyabensis*), occur in the mountain range (J. Brack personal communication).

More than 99% of the Toquima Range is federally owned. The U.S. Forest Service oversees 88% of the range, and the Bureau of Land Management controls 11% (BRRC 1997). Thus, the majority of income-generating activities in the Toquima Range, including livestock grazing and mining, must be approved by the appropriate federal agency. This has caused considerable conflict between agencies and some local residents, who contend that the rightful owners of public lands are the counties rather than the federal goverment (Egan 1995, Larson 1995, USFS 1995). Two of the most publicized battles in the recent history of the "Sagebrush Rebellion" have been fought in the Toquima Range—the unauthorized opening (by bulldozer) of a Forest Service road in Jefferson Canyon by Nye County Commissioner Dick Carver, and the Forest Service's impoundment of cattle owned by rancher Wayne Hage in Pine Creek Canyon.

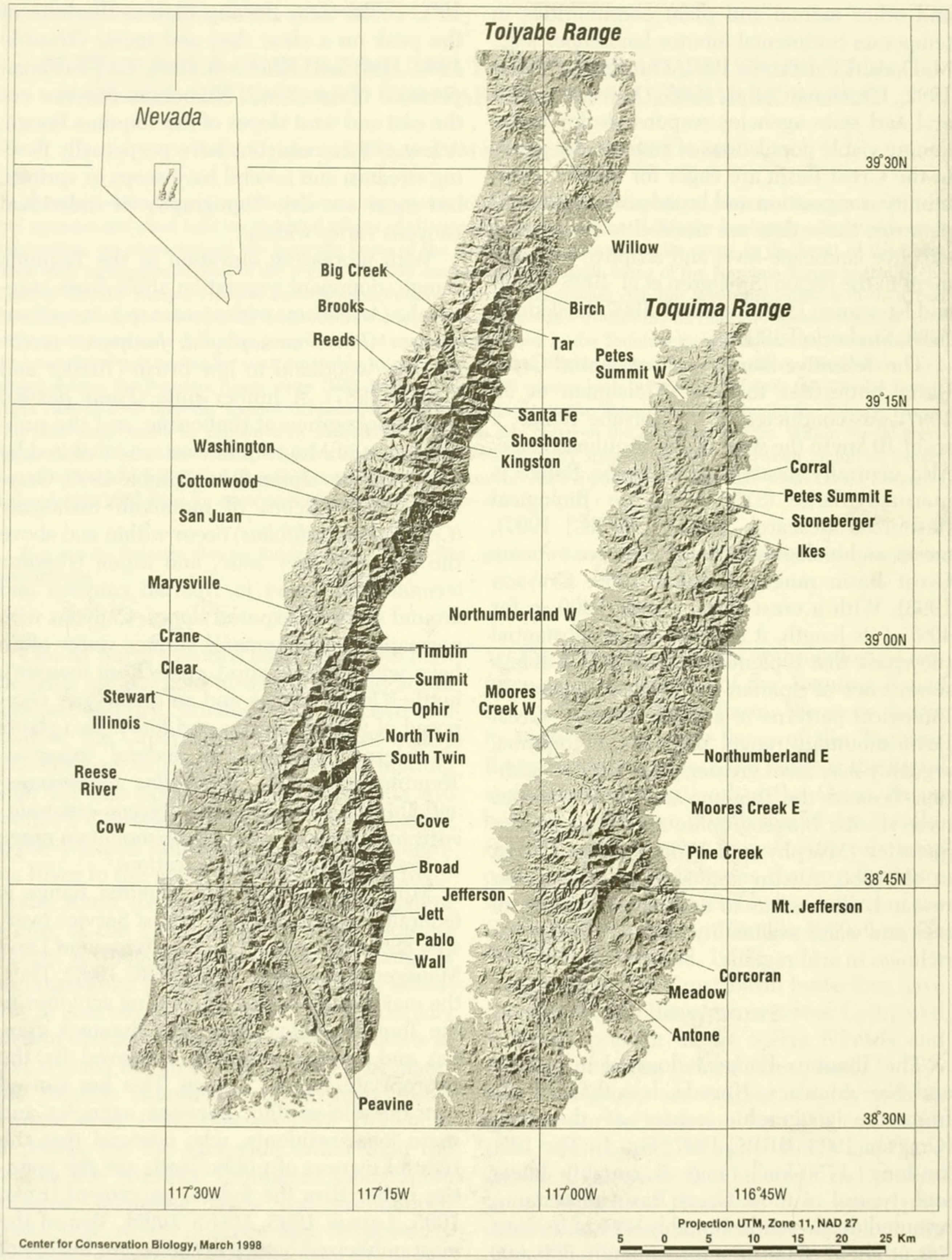

Fig. 1. Study canyons in the Toquima and Toiyabe ranges and their position within Nevada (inset).

METHODS

We compiled species presence data for 14 canyons in the Toquima Range and for Mount Jefferson from specimens in private and institutional collections, field notes of experienced lepidopterists, a systematic inventory conducted in the mid-1980s, and a systematic inventory conducted in 1996 and 1997. One canyon was included in the 1980s inventory, and 10 canyons were included in the 1990s inventory (Fig. 1). Five canyons were inventoried in both 1996 and 1997, 4 in 1996 only, and 1 in 1997 only. To account for differences in flight phenology among species and locations, we inventoried each canyon roughly every 2 wk throughout the majority of the flight season (May–August). During canyon visits we walked the length of each canyon at a constant pace and recorded presence of all butterfly species seen. Walking transects are a standard technique for surveying butterfly communities (Shapiro 1975, Pollard 1977, Thomas and Mallorie 1985, Swengel 1990, Kremen 1992, Pollard and Yates 1993, Harding et al. 1995). When necessary, individual butterflies were caught and either identified on site or held for later identification. Voucher specimens were deposited at the University of Nevada, Reno and at the Nevada State Museum and Historical Society, Las Vegas. Our nomenclature largely follows that of Austin (in press).

We did not attempt to quantify abundances of all butterfly species recorded from the Toquima Range because, particularly over a relatively short (2-yr) time period, estimation of abundance is complicated by factors including interspecific variation in population structure, sensitivity to short-term climatic fluctuations, and staggered emergence (Shapiro 1975, Scott 1986). However, we did categorize each butterfly species with respect to its qualitative relative abundance in its principal habitat at the peak of its flight season in the Toquima Range (Fleishman et al. 1997). We established 6 relative abundance categories: abundant (generally seen and in large numbers), common (generally seen but not in large numbers), fairly common (generally seen but in small numbers or not generally seen), uncommon (seldom seen but not a surprise), rare (presence always a surprise but not far out of normal range), and accidental (far out of normal range).

Toquima Range canyons are frequently narrow and steeply walled. Canyon bottoms are the most accessible areas in the Toquima Range, and virtually all resident butterflies in the Toquima Range occur there (Fleishman et al. 1997). Therefore, we defined the area that our transects sampled ("canyon area") as 50 m on either side of the inventory route. To calculate this area, we recorded the location of our 1990s inventory transects with differentially corrected Global Positioning Systems (GPS), which are accurate within 5 m. GPS positions were then overlaid on a 30-m Digital Elevation Model of the central Great Basin maintained on a Geographic Information System (GIS).

We used analysis of variance to test whether there was a significant difference in mean number of species and canyon area among Toquima Range and Toiyabe Range canyons that were inventoried systematically over the past 4 yr (1994–1997). Eleven Toquima Range canyons and 19 Toiyabe Range canyons were included in these tests (see Fig. 1). The same methods were used to inventory Toiyabe Range and Toquima Range canyons. A detailed description of Toiyabe Range natural history, study locations, and inventory results is presented in Fleishman et al. (1997).

RESULTS

Eighty butterfly species have been recorded from the Toquima Range since 1935 (Table 1). Species richness of individual canyons ranged from a high of 66 species in Meadow Canyon to a low of 26 in Corral Canyon. Twenty-seven species have been recorded from Mount Jefferson. Species richness of the 11 canyons we inventoried systematically ranged from 66 (Meadow Canyon) to 33 (Petes Summit West), with a mean of 50. Of the latter group of canyons, 5 have flowing streams, 5 have localized seeps or springs, and 1 is dry (Table 1).

Fifty-nine butterfly species recorded from the Toquima Range most likely are resident, i.e., complete their entire life cycle in the Toquima Range (Table 2). Of these species, 25 are restricted to montane habitats and do not occur in valleys in the vicinity of the Toquima Range (Table 2). Two species that occur regularly in the Toquima Range, *Vanessa cardui* and *Danaus plexippus*, are true migrants (Scott 1986). Some individuals of 1 resident species (*Nymphalis antiopa*) may migrate. An additional 18 species are frequent or infrequent

TABLE 1. Canyon-level butterfly distribution records, Toquima Range, Lander and Nye counties, Nevada. Water codes: 1 = flowing stream, 2 = seep or spring. Location codes: PW = Petes Summit, west side; NW = Northumberland, west side; MW = Moores Creek, west side; JF = Jefferson; PT = Petes Summit, east side; CA = Corral; SB = Stoneberger; IK = Ikes; NE = Northumberland, east side; ME = Moores Creek, east side; PI = Pine Creek; CN = Corcoran; AN = Antone; MD = Meadow; MJ = Mount Jefferson.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Resident															
HESPERIIDAE															
Erynnis icelus (Scudder & Burgess)															x
Erynnis persius (Scudder)	x	x		x	x	x	x	x	x		x		x	x	
Hesperia uncas W.H. Edwards ssp.	x	x	x	x	x	x	x	x		x				x	x
Hesperia juba (Scudder)	x	x	x	x	x	x	x	x	x	x		x	x	x	
Hesperia comma harpalus (W.H. Edwards)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Ochlodes sylvanoides bonnevilla Scott		x	x	x			x		x	x		x	x	x	
PAPILIONIDAE															
Papilio zelicaon Lucas				x										x	x
Papilio indra nevadensis T. & J. Emmel				x							x				
Papilio rutulus rutulus Lucas		x	x	x	x	x	x	x		x	x	x	x	x	x
Papilio multicaudatus W.F. Kirby ssp.				x			x				x	x	x	x	
PIERIDAE															
Neophasia menapia (C. & R. Felder) ssp.	x	x	x	x	x		x		x			x		x	
Pontia beckerii beckerii (W.H. Edwards)	x	x	x	x	x		x	x	x	x		x	x	x	
Pontia sisymbrii elivata (Barnes & Benjamin)		x					x							x	
Euchloe ausonides (Lucas) ssp.		x	x	x	x			x							
Euchloe hyantis lotta Beutenmüller			x				x						x		
Anthocharis sara thoosa (Scudder)			x		x	x	x						x	x	
Colias philodice eriphyle W.H. Edwards							x							x	
Colias alexandra edwardsii W.H. Edwards	x	x	x	x	x		x	x	x	x	x	x	x	x	x
LYCAENIDAE															
Lycaena arota virginiensis (W.H. Edwards)				x					x	x		x		x	
Lycaena rubidus sirius (W.H. Edwards)							x	x				x	x	x	
Lycaena heteronea Boisduval ssp.		x	x	x				x	x	x	x		x	x	
Lycaena helloides helloides (Boisduval)				x	x	x	x						x		
Harkenclenus titus immaculosus (W.P. Comstock)														x	
Satyrium behrii crossi (Field)	x	x	x	x	x		x		x	x		x	x	x	

TABLE 1. Continued.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Satyrium californicum (W.H. Edwards) ssp.				x	x			x		x			x	x	
Satyrium sylvinum putnami (Hy. Edwards)			x	x	x		x					x	x	x	
Callophrys affinis affinis (W.H. Edwards)		x	x	x	x				x	x	x		x	x	x
Loranthomitoura spinetorum spinetorum (Hewitson)	x	x			x						x				
Mitoura siva chalcosiva (Clench)	x	x	x	x	x		x		x	x				x	
Incisalia eryphon (Boisduval) ssp.	x	x	x	x	x		x		x	x	x	x	x	x	
Everes amyntula herrii F. Grinnell		x		x	x		x		x	x	x			x	
Celastrina ladon echo (W.H. Edwards)							x			x	x			x	
Euphilotes enoptes (Boisduval) ssp.	x	x		x	x	x	x		x	x	x		x	x	x
Glaucopsyche piasus nevada F.M. Brown				x		x	x		x	x	x	x	x	x	x
Glaucopsyche lygdamus oro (Scudder)		x		x						x					
Lycaeides melissa paradoxa (F.H. Chermock)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Plebejus saepiolus (Boisduval) ssp.		x	x	x		x	x	x		x	x	x	x	x	x
Icaricia icarioides fulla (W.H. Edwards)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Icaricia shasta (W.H. Edwards) ssp.		x	x	x			x	x	x	x	x		x	x	x
Icaricia acmon texana (Goodpasture)					x	x	x	x	x	x	x			x	x
Icaricia lupini (Boisduval) ssp.	x	x	x	x	x	x	x		x	x	x	x	x	x	x
Apodemia mormo mormo (C. & R. Felder)	x	x	x	x	x		x		x	x		x		x	
NYMPHALIDAE															
Speyeria coronis snyderi (Skinner)		x			x										
Speyeria zerene gunderi (J.A. Comstock)		x	x				x		x			x	x	x	
Speyeria callippe harmonia dos Passos & Grey	x	x		x	x	x	x	x	x				x	x	x
Thessalia leanira alma (Strecker)	x				x										
Chlosyne acastus acastus (W.H. Edwards)		x	x	x		x	x	x	x	x	x	x	x	x	
Phyciodes pulchella (Boisduval) ssp.		x	x	x		x	x	x			x		x	x	
Phyciodes mylitta mylitta (W.H. Edwards)				x			x		x		x	x	x	x	
Euphydryas anicia wheeleri (Hy. Edwards)	x	x	x	x	x	x	x	x	x	x		x	x	x	
Euphydryas editha lehmani Gunder	x	x	x	x	x	x	x	x	x	x			x	x	x

TABLE 1. Continued.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Polygonia zephyrus (W.H. Edwards)		x	x	x			x				x	x	x	x	x
Nymphalis antiopa antiopa (Linnaeus)	x	x	x	x	x	x	x	x			x	x	x	x	
Nymphalis milberti subpallida (Cockerell)		x				x	x			x	x			x	x
Limenitis weidemeyerii latifascia E.M. & S.F. Perkins	x	x	x	x	x		x	x	x	x	x	x	x	x	
Coenonympha tullia (Müller) spp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cercyonis sthenele paulus (W.H. Edwards)	x	x	x	x	x		x		x	x	x	x	x	x	
Cercyonis oetus oetus (Boisduval)	x	x	x	x		x	x	x	x	x	x	x	x	x	x
Neominois ridingsii stretchii (W.H. Edwards)	x	x	x	x	x		x	x	x	x				x	
SUBTOTAL	26	41	35	45	35	23	46	26	33	35	30	29	38	50	22
Migrant or Immigrant															
HESPERIIDAE															
Pyrgus scriptura (Boisduval) ssp.		x		x											
Pyrgus communis communis (Grote)	x	x	x	x	x		x		x	x		x	x	x	
Heliopetes ericetorum (Boisduval)		x											x	x	
PIERIDAE															
Pontia protodice (Boisduval & Le Conte)	x	x	x	x	x		x		x	x	x	x	x	x	
Pontia occidentalis occidentalis (Reakirt)	x	x						x						x	x
Pieris rapae rapae (Linnaeus)														x	
Colias eurytheme Boisduval	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Nathalis iole Boisduval							x								
LYCAENIDAE															
Strymon melinus pudica (Hy. Edwards)		x	x	x									x	x	
Leptotes marina (Reakirt)			x							x	x			x	x
Brephidium exilis exilis (Boisduval)		x	x	x	x					x	x	x	x	x	
Hemiargus isola alce (W.H. Edwards)										x					
NYMPHALIDAE															
Vanessa virginiensis (Drury)							x							x	
Vanessa cardui (Linnaeus)	x	x	x		x	x	x			x	x		x	x	x
Vanessa annabella (Field)		x				x	x	x						x	x
Vanessa atalanta rubria (Fruhstorfer)							x				x			x	
Junonia coenia Hübner	x														

TABLE 1. Continued.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Danaus plexippus plexippus (Linnaeus)		x		x			x	x		x		x	x	x	
SUBTOTAL	6	11	7	7	5	3	9	4	3	8	6	5	8	14	5
Marginal or Accidental															
HESPERIIDAE															
Hesperopsis libya lena (W.H. Edwards)	x	x	x												
PAPILIONIDAE															
Battus philenor philenor (Linnaeus)														x	
PIERIDAE															
Eurema mexicana mexicana (Boisduval)							x							x	
SUBTOTAL	1	1	1				1							2	
TOTAL	33	53	43	52	40	26	56	30	36	43	36	34	46	66	27

immigrants to the Toquima Range (whether or not the species breed in the Toquima, they probably cannot survive all winters in the range; Table 2). *Hesperopsis libya* sometimes strays into the Toquima Range from Big Smoky Valley to the west; there may be some localized populations of the species on the west slope of the Toquima Range. Single *Battus philenor* and *Eurema mexicana*, well outside their usual distributional range (Scott 1986), have been recorded from the Toquima Range.

Fourteen species recorded from the Toquima Range, including 13 residents, are riparian obligates (Table 2). We define riparian obligate species as those that could not maintain permanent populations in the absence of a riparian zone because their larval host plants do not or rarely occur away from dependable water (Fleishman et al. 1997).

Of 59 resident butterfly species in the Toquima Range, 8 are abundant. Ten resident and 1 immigrant species are common. A total of 28 species, 23 resident and 5 migrant or immigrant, are fairly common. Eleven resident, 5 migrant or immigrant, and 1 marginal species are uncommon, while 14 species (7 resident and 7 immigrant) are rare.

All resident butterfly species and all but 3 nonresident species (*Pyrgus scriptura*, *B. philenor*, and *E. mexicana*) recorded from the Toquima Range also have been recorded from the Toiyabe Range. In a previous paper (Fleishman et al. 1997), we presented data on the life history of Toiyabe Range butterflies. Most data that are applicable across the 2 mountain ranges are not repeated here. These data included each species' geographic distribution (relative position of the Toquima Range within its geographic range and its subspecific-level biogeographic affinity), potential host plants in the Toquima Range, relative annual fluctuation in abundance, habitat in which the butterfly most frequently is observed (including riparian canyons, all canyons, and uplands), and habitat use (patrolling habitat, perching habitat, and relative use of mud puddles).

The mean number of species recorded from Toquima Range canyons was significantly less than the mean number of species recorded from systematically inventoried Toiyabe Range canyons. This result was consistent for resident species (Toquima mean = 37, Toiyabe mean = 48, $F_{.05[1,27]} = 11.029$, $P < 0.005$), nonresident species (Toquima mean = 8, Toiyabe mean = 13, $F_{.05[1,27]} = 9.832$, $P < 0.005$), and all species (Toquima mean = 45, Toiyabe mean = 61, $F_{.05[1,27]} = 11.622$, $P < 0.005$). Although species richness tends to increase with canyon area in

TABLE 2. Life history traits of butterflies recorded from the Toquima Range. Montane species are restricted to montane habitats; individuals of these species rarely if ever occur in valleys in the Toquima Range vicinity. Riparian obligate species are those that could not maintain permanent populations in the absence of a riparian zone because their larval host plants do not or rarely occur away from dependable water. Relative abundance categories are abundant (generally seen and in large numbers), common (generally seen but not in large numbers), fairly common (generally seen but in small numbers or not generally seen), uncommon (seldom seen but not a surprise), rare (presence always a surprise but not far out of normal range), and accidental (far out of normal range).

Species	Montane	Riparian obligate	Relative abundance
RESIDENT			
Erynnis icelus	x	x	rare
Erynnis persius	x		uncommon
Hesperia uncas	x		fairly common
Hesperia juba			abundant
Hesperia comma			abundant
Ochlodes sylvanoides			fairly common
Papilio zelicaon	x		rare
Papilio indra	x		rare
Papilio rutulus	x	x	fairly common
Papilio multicaudatus	x	x	fairly common
Neophasia menapia	x		common
Pontia beckerii			common
Pontia sisymbrii	x		uncommon
Euchloe ausonides	x		fairly common
Euchloe hyantis			uncommon
Anthocharis sara	x		fairly common
Colias philodice		x	uncommon
Colias alexandra			common
Lycaena arota	x		fairly common
Lycaena rubidus		x	fairly common
Lycaena heteronea	x		common
Lycaena helloides		x	uncommon
Harkenclenus titus	x	x	rare
Satyrium behrii	x		fairly common
Satyrium californicum	x		fairly common
Satyrium sylvinum		x	fairly common
Callophrys affinis	x		uncommon
Loranthomitoura spinetorum	x		rare
Mitoura siva	x		fairly common
Incisalia eryphon	x		common
Everes amyntula			fairly common
Celastrina ladon	x		uncommon
Euphilotes enoptes	x		fairly common
Glaucopsyche piasus	x		fairly common
Glaucopsyche lygdamus			fairly common
Lycaeides melissa			common
Plebejus saepiolus		x	uncommon
Icaricia icarioides	x		abundant
Icaricia shasta	x		common
Icaricia acmon			uncommon
Icaricia lupini	x		fairly common
Apodemia mormo			common
Speyeria coronis	x		rare
Speyeria zerene	x		fairly common
Speyeria callippe	x		uncommon
Thessalia leanira	x		rare
Chlosyne acastus	x		abundant
Phyciodes pulchella	x		fairly common
Phyciodes mylitta			fairly common
Euphydryas anicia	x		abundant
Euphydryas editha	x		fairly common
Polygonia zephyrus	x		fairly common
Nymphalis antiopa	x		fairly common
Nymphalis milberti	x		uncommon

TABLE 2. Continued.

Species	Montane	Riparian obligate	Relative abundance
Limenitis weidemeyerii			common
Coenonympha tullia			abundant
Cercyonis sthenele	x		abundant
Cercyonis oetus			abundant
Neominois ridingsii	x		common
MIGRANT OR IMMIGRANT			
Pyrgus scriptura			rare
Pyrgus communis			fairly common
Heliopetes ericetorum			common
Pontia protodice			fairly common
Pontia occidentalis			uncommon
Pieris rapae	x		uncommon
Colias eurytheme			fairly common
Nathalis iole			rare
Strymon melinus			rare
Leptotes marina			rare
Brephidium exilis			fairly common
Hemiargus isola			rare
Vanessa virginiensis			rare
Vanessa cardui			uncommon
Vanessa annabella			uncommon
Vanessa atalanta	x		rare
Junonia coenia			uncommon
Danaus plexippus			fairly common
MARGINAL OR ACCIDENTAL			
Hesperopsis libya			uncommon
Battus philenor			accidental
Eurema mexicana			accidental

both ranges (Fleishman et al. unpublished manuscripts), the mean area of Toquima and Toiyabe Range canyons was not significantly different (Toquima mean = 99.2 ha, Toiyabe mean = 85.7 ha, $F_{.05[1,21]} = 1.222$, $P = 0.28$). In other words, the difference in species richness between Toquima and Toiyabe Range canyons cannot be explained by differences in canyon size between the 2 ranges.

DISCUSSION

Knowledge of species distributions and coarse-grained species richness patterns is critical to conservation planning exercises including reserve design, land-use decision making, and adaptive management (Doak and Mills 1994, Stohlgren et al. 1995, Lambeck 1997, Longino and Colwell 1997, Mac Nally 1997, Simberloff 1998). Documenting butterfly distributions not only has intrinsic merit, but also could prove valuable because butterflies widely are thought to be sensitive to anthropogenic disturbances and able to provide an early warning of ecological change (Noss 1990, Kremen et al. 1993, New et al. 1995, Hamer et al. 1997).

Within the Toquima Range, moisture appears to be a primary factor affecting butterfly species richness at the canyon level. Water may enhance plant species richness and help both to prolong the temporal window for plant growth and flowering and to maintain muddy patches used by adult butterflies (Murphy and Wilcox 1986). Of the 11 canyons we inventoried systematically, the 2 with the greatest number of resident butterfly species have running streams, and the 8 richest canyons all have either running streams or seeps. Canyons rich in butterflies also tend to be topographically heterogeneous; thus, they tend to have diverse microclimatic zones and plant communities as well as sites for perching and patrolling by butterflies.

Several interacting factors, including area, moisture, and topography, probably contribute to species richness at the level of mountain ranges. The effects of area on species richness may be more significant at the level of mountain ranges than at the level of canyons. Thus, the larger area of the Toiyabe Range relative to the Toquima Range as a whole (as opposed to the area of their constituent canyons) may help explain why more butterfly species occupy the Toiyabe than the Toquima Range. Often, as is the case with the Toiyabe and Toquima ranges, larger ranges have greater topographic and vegetational diversity than smaller ranges (Grayson 1993). In addition, larger ranges might have, on average, more populations per species than smaller ranges, which decreases the risk of stochastic species extirpations within mountain ranges (Gilpin and Soulé 1986, Rabinowitz et al. 1986).

The difference in moisture availability between the Toquima and Toiyabe ranges, which is driven partly by their topographic differences, also may help explain why the Toquima Range has fewer butterfly species than the Toiyabe Range. In the Great Basin, ranges like the Toquima that are moderately small and low tend to be more arid than relatively large and tall ranges (e.g., the Toiyabe Range). Annual precipitation estimates obtained from the orographic precipitation model PRISM (Parameter-elevation Regressions on Independent Slopes Model; Daly et al. 1994) indicate that annual precipitation in a given canyon in the Toquima Range is not substantially less than precipitation in a given canyon in the Toiyabe Range. However, crests of larger and higher ranges capture more winter snow (which accounts for most of the effective precipitation in the Great Basin; Trimble 1989, Hidy and Klieforth 1990, Grayson 1993) and retain their snowpack later in the year than do smaller ranges. Gradual snowpack melting appears to replenish streams and may delay vegetation senescence, including larval host plants and adult nectar sources.

Eleven resident butterfly species recorded from the Toiyabe Range have not been recorded from the Toquima Range. There are parsimonious explanations for most of these apparent absences. Distributions of 4 species recorded from the Toiyabe but not the Toquima, *Pholisora catullus*, *Lycaena nivalis*, *Incisalia augustinus*, and *Speyeria egleis*, are either relictual or indicative of more recent dispersal from elsewhere, probably the northeastern Great Basin (Fleishman et al. 1997). The Toiyabe Range is the only central Great Basin location in which these 4 species have been recorded. Similarly, the only central Great Basin record of *Lycaena editha* is from the Toiyabe. An isolated population of *Ochlodes yuma* is associatied with a small patch of its host plant, *Phragmites australis*, on the east slope of the Toiyabe Range (Fleishman et al. 1997). Although there are several records of *Callophrys comstocki* and *Polygonia satyrus* from the Toiyabe Range, we did not encounter either species in that range during butterfly inventories in the 1990s. Likewise, only 1 *Euphilotes battoides* was recorded from the Toiyabe Range in the 1990s. Finally, the apparent absence of *C. comstocki*, *E. battoides*, and *Incisalia fotis* may reflect sampling error. These 3 species fly extremely early in the season and are rare.

Two species remain whose apparent absence from the Toquima Range is surprising—*Papilio bairdii* and *Speyeria nokomis*. Host plants and habitat that seem suitable for both species occur in the Toquima Range. However, both species principally are found in riparian canyons; streams and seeps in the Toquima Range often are isolated. Suitable habitat patches in the Toquima Range may be too distant from each other and from occupied habitats outside the range for immigration to occur regularly and for the species to maintain viable populations in the Toquima Range (Murphy et al. 1990, Hanski 1991, Hanski and Gilpin 1991).

Examination of species richness and composition within and among mountain ranges can have a significant bearing on management of rugged, remote landscapes like the Great Basin. Knowledge of "what is where" and why some areas have more species than others (particularly if species richness responds to factors that can be influenced by management) is critical to scientifically informed conservation planning. Not only do distributional data assist managers in delineating land uses, but they also can help managers and researchers predict and evaluate effects of experimental management strategies such as prescribed burning or alternative grazing schemes. The ecology of the Toquima Range may elicit few superlatives, but this very fact makes the range an excellent model for examining Great Basin species distributions across spatial scales critical to conservation planning.

ACKNOWLEDGMENTS

We thank P.F. Brussard, C.L. Boggs, A.E. Launer, and 2 anonymous reviewers for many helpful comments on the manuscript. Numerous lepidopterists contributed records. Thanks to A. Weiss, R. Bamford, T. Wade, and J. Fay for computer support, including preparation of figures. The Austin and Tonopah ranger districts of the Humboldt-Toiyabe National Forest provided substantial logistic support in the field. Logistic support also was provided by the Biological Resources Research Center (University of Nevada, Reno). Research was funded by the Nevada Biodiversity Research and Conservation Initiative, Nevada State Museum and Historical Society, and Center for Conservation Biology. Activities conducted under Challenge Cost-Share Agreement 17-CSS-97-016 between the U.S. Forest Service and the University of Nevada, Reno also contributed to this manuscript. This is Contribution Number 57 of the Nevada Biodiversity Initiative.

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Received 18 December 1997
Accepted 8 May 1998