Herpetological Conservation and Biology 6(1):61−71.
Submitted: 17 February 2010; Accepted: 19 March 2011.

SONORAN DESERT SNAKE COMMUNITIES AT TWO SITES: CONCORDANCE AND EFFECTS OF INCREASED ROAD TRAFFIC

***THOMAS R. JONES*[1], *RANDALL D. BABB*[2], *FRANK R. HENSLEY*[3], *CHRISTINE LIWANPO*[4], *AND BRIAN K. SULLIVAN*[5]**

[1]*Nongame Branch, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, Arizona 85086*, USA
[2]*Arizona Game and Fish Department, 7200 East University, Mesa, Arizona 85207*, USA
[3]*Department of Biology, Trinity Christian College, 6601 W. College Drive, Palos Heights, Illinois 60463*, USA
[4]*Midwestern University Arizona College of Osteopathic Medicine, Glendale, Arizona 85308*, USA
[5]*Division of Mathematical and Natural Sciences, Arizona State University, PO Box 37100, Phoenix, Arizona 85069 USA,e-mail:bsullivan@asu.edu*

***Abstract.*—We surveyed the snake communities at two locations in the Sonoran Desert of southcentral Arizona. From 1982–2009, we used roadways as sampling transects and recorded all snakes detected during nights at a predominately Lower Colorado River Valley subdivision community south of Phoenix and at a primarily Arizona Upland subdivision community west of Phoenix. The snake communities were largely concordant both in diversity and abundance of species at these Sonoran Desert sites: four species (*Crotalus cerastes, C. atrox, C. scutulatus,* and *Rhinocheilus lecontei*) accounted for 67–70% of all individuals at the two sites. The most common species exhibited similar distributions at both of the sites with respect to habitat adjacent to the roadway. Following a dramatic upsurge in traffic volume at both sites in the past decade, the abundance of all snakes declined at one site, and the proportion of dead snakes increased significantly at the other site. Comparison with other road-riding surveys of snake communities in the American Southwest indicates that this technique provides consistent and repeatable results, and that this method suggests similar species numerically dominate snake communities in the Sonoran Desert of Arizona.**

Key Words.—Arizona; community structure; desert biomes; road riding; snakes; Sonoran Desert; traffic

INTRODUCTION

The community ecology of squamate reptiles, especially of arid regions, has received considerable attention, with lizards having long served as model organisms for elucidating a variety of ecological principles (Pianka 1986). Snakes have been the subject of far fewer studies, in part because of the difficulty of surveying populations and obtaining data on diversity and abundance of these reclusive reptiles. Recent analyses of snake community structure from temperate and tropical biomes suggest that snakes may play important roles as mesopredators and warrant consideration from a conservation perspective, their poor image among nonscientists notwithstanding (reviewed by Luiselli 2007). In a study of forest biomes and farmland mosaic in New England, Kjoss and Litvaitis (2001) documented that large snakes, in part as a result of preference for larger habitat patches, affected abundance of smaller snake species directly through predation. Thus, interactions among snakes influencing community structure are complex, and complicate conservation efforts for these reptiles. Despite these recent investigations, snakes of arid environments remain little studied, especially with respect to widespread anthropogenic effects (Sullivan et al. in press).

In spite of the difficulties of accurately censusing snakes, since the 1920s it has been recognized that many snake species can be surveyed effectively by driving a motor vehicle slowly on a paved road during the early evening in spring and summer (e.g., Klauber 1939; Bugbee 1945; Hensley 1950; Pough 1966). In contrast to the effort required to observe snakes under more natural conditions, snakes found dead on the road (DOR) as well as alive (AOR) can be counted in large numbers during a few short survey hours using road riding. In a number of studies of snake communities, road riding was the only sampling technique used, with paved roads functioning as "transects" through the habitat (e.g., Sullivan 1981a, 2000; Mendelson and Jennings 1992). This method is commonly employed by collectors of reptiles and amphibians to obtain specimens for the pet-trade and other purposes (Sullivan 2000). Snakes of arid and semi-arid regions of the southwestern USA have been the focus of most road riding studies (e.g., Sullivan 1981a; Price and LaPointe 1990; Rosen and Lowe 1994). Snakes may be found on roadways by chance, or because they use paved road surfaces, which retain heat, for thermoregulation in the early evening during spring

FIGURE 1. Arizona Upland subdivision of the Sonoran Desert at the 2 km mark of the SVP transect showing the proximity of the White Tank Mountains to the roadway (upper panel). Lower Colorado River Valley subdivision of the Sonoran Desert at the 20 km mark of the SVP transect showing the sandy floodplain of the Hassayampa River to the west (lower panel; both photographs by Brian Sullivan).

FIGURE 2. Lower Colorado River Valley subdivision of the Sonoran Desert at the 25 km mark of the MR-238 transect showing extensive creosote flats (upper panel). Arizona Upland subdivision of the Sonoran Desert at the 45 km mark of the MR-238 transect showing the proximity of the Maricopa Mountains (lower panel; both photographs by Brian Sullivan).

and summer (Sullivan 1981b); snakes may also bask on both surfaced and unsurfaced roadways during daylight hours.

In an analysis of snake communities of Chihuahuan Desert and grassland biotic communities in southeastern Arizona and southwestern New Mexico, Mendelson and Jennings (1992) used road riding to survey two roads that had been sampled roughly 25 years previously (Pough 1966). They documented significant shifts in relative abundance of some taxa, and detected some small, secretive snake species unobserved by Pough. In a similar fashion, Dodd et al. (1989) questioned the efficacy of road riding as a sampling technique because they encountered only 11 species of small, terrestrial snakes on the roadway out of the 22 known to occur in the immediate vicinity in Alabama. Langen et al. (2007) documented that small snakes sometimes missed during vehicular surveys were detected during pedestrian surveys along the same route in New York, supporting the view that detection of small individuals can depend on the survey methods, road conditions, and personnel. Road riding as a sampling technique must be used with caution, and analysis of consistency in this method would allow assessment of its validity (Sullivan in press).

We used road riding to examine the distribution and abundance of snakes found on two roadways in the Sonoran Desert of south-central Arizona. One road was situated along the bajada (coalesced alluvial fans) of a mountain range primarily in the Arizona Upland subdivision of the Sonoran Desert (Fig. 1; Turner and Brown 1982), while the other crossed a relatively broad valley, passing primarily through the Lower Colorado River Valley subdivision of the Sonoran Desert (Fig. 2; Turner and Brown 1982). We assessed the concordance of these two communities in diversity and abundance of snake species, and in response to increasing anthropogenic activities, both in the form of direct mortality from increased road traffic, and indirect effects

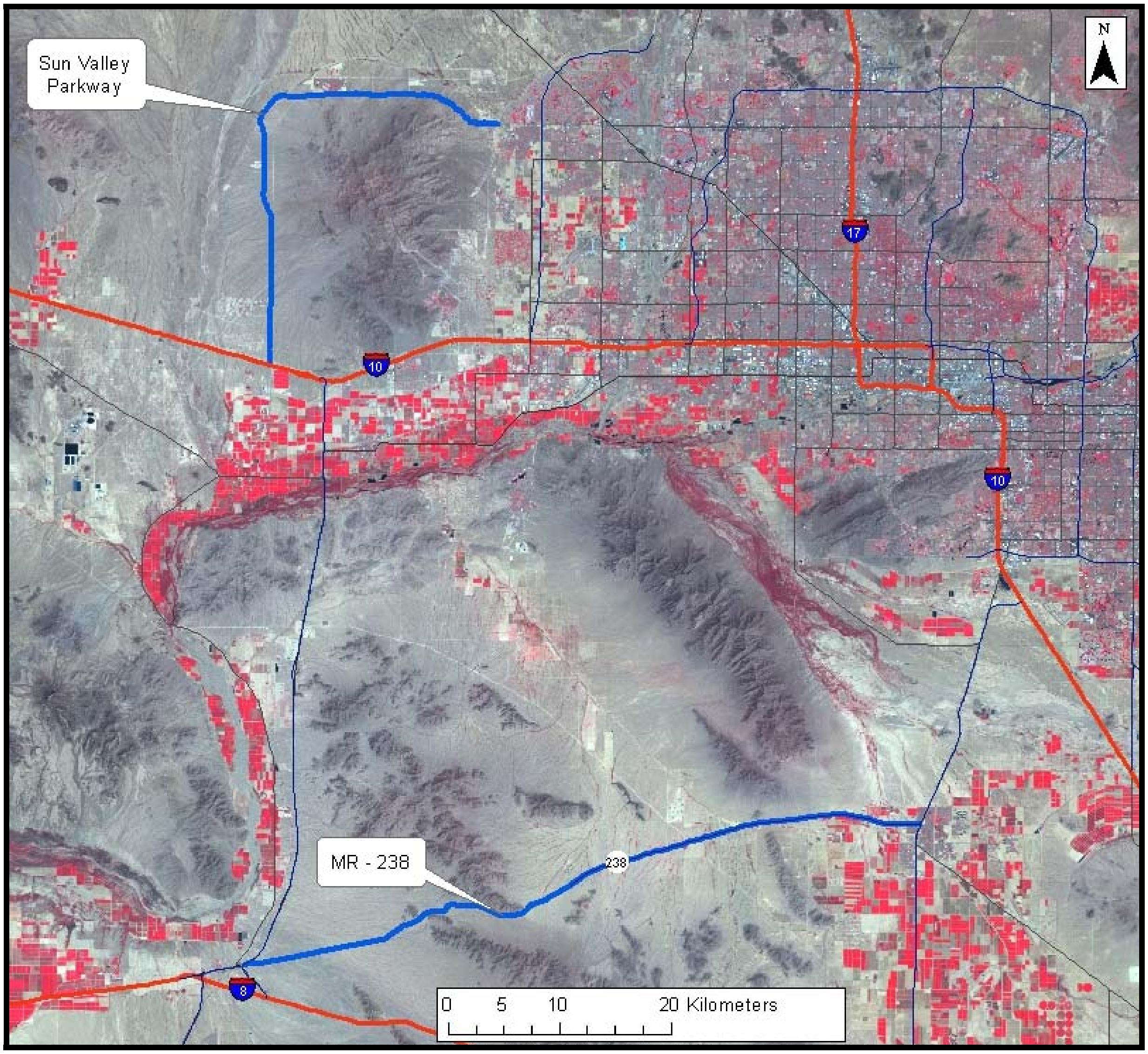


FIGURE 3. Aerial image of the Sun Valley Parkway (SVP; west of Phoenix) and MR-238 (southwest of Phoenix) study sites. Note the extensive washes crossing MR-238 and the bajada (alluvial fans forming a skirt of deposits that surround many desert mountain ranges) habitat associated with SVP. In addition, recent development is shown in grey and white along the upper edge of SVP, west of the White Tank Mountains (figure is a modified Landsat 5 image, acquired 26 August 2009, maximizing contrast for vegetation, shown in pink/red).

associated with off-road habitat modification due to development.

MATERIALS AND METHODS

Because road riding is thought to be most successful on dark, windless nights during the peak activity period of target organisms (Sullivan in press), we did not randomly select survey nights across seasons for the Sun Valley Parkway (hereafter, SVP): we conducted surveys at this site during the early evening from mid-April to late September, 1998–2009. During the summer months, we often conducted surveys during and after rainstorms. However, for the Maricopa Road (hereafter, MR-238, reflecting that the eastern portion of the road is State Route 238), surveys reported herein were conducted opportunistically during the night from April to September, 1982–2006. At both sites, we conducted most surveys from sunset (typically 1800 to 2000) until activity declined (approximately 2300) by passing through the site once or twice in a vehicle traveling approximately 25–45 kph, with at least one observer (often more) in addition to the driver in the vehicle. SVP was relatively new (dark pavement) during the early survey years, but MR-238 was unpaved during the initial surveys (1982–1987; N = 18 surveys), paved for

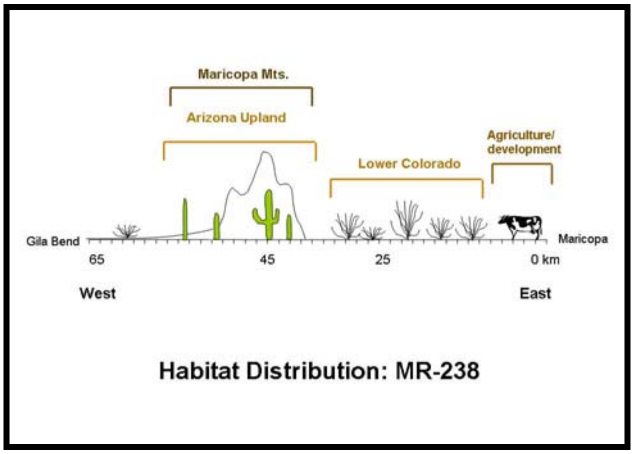


FIGURE 4. Depiction of habitat variation along MR-238, near Phoenix, Arizona, USA.

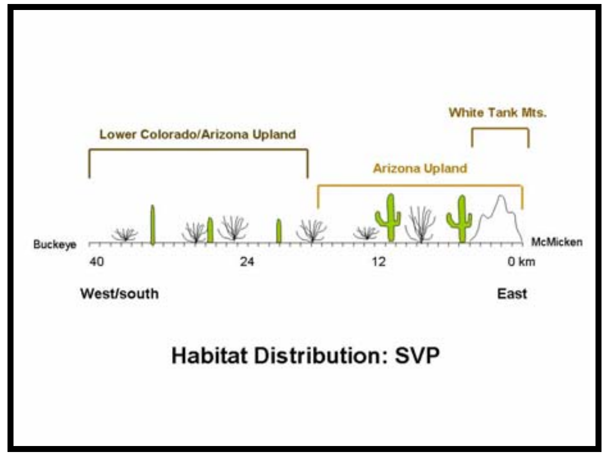


FIGURE 5. Depiction of habitat variation along SVP, near Phoenix, Arizona, USA.

the first 33 km from 1988 to 1999 (N = 34 surveys), and over its entire length from 2000 to 2006 (N = 28 surveys). We recorded each snake as alive (AOR) or dead (DOR), and we noted the location to the nearest tenth of a mile (= 0.16 km) west of the starting point (the intersection of state routes 238 and 347 for MR-238; McMicken Dam for SVP).

Study sites.—The MR-238 site is located between 50 and 65 km south and southwest of Phoenix, in Maricopa and Pinal cos., Arizona, USA, while the SVP site is 65 km west of Phoenix, entirely within Maricopa Co.; roughly 65 km separate the two sites. MR-238 was surveyed from the town of Maricopa, Pinal Co. (UTM: 12S, 402335 E, 3659632 N, NAD Conus, 1927), west 65 km to the junction with state route 85 in Gila Bend, Maricopa Co. (12S, 341741 E, 347031 N; Figs. 3, 4). After MR-238 was paved in 1988, we largely restricted surveys to the paved section of the road. Thus, we conducted the majority of surveys on MR-238 over these first 33 km from the town of Maricopa to the end of state route 238, east of the pass through the North and South Maricopa mountains.

The survey area along MR-238 included developed land at the easternmost edge (agricultural and housing) in historically Lower Colorado River Valley subdivision (i.e., Creosote flats), dominated by Triangle-leaf Bursage (*Ambrosia deltoidea*), White Bursage (*A. dumosa*) and Creosote (*Larrea tridentata*). Roughly 36 km west of Maricopa, the roadway entered a wide pass between the North and the South Maricopa mountains for 10 km, primarily Arizona Upland subdivision characterized by Saguaro Cactus (*Carnegiea gigantea*), Ocotillo (*Fouquieria splendens*), Foothill Palo Verde (*Parkinsonia microphylla*), and Brittlebush (*Encelia farinosa*); west of the Maricopa Mountains, the roadway was again associated with Lower Colorado River Valley subdivision Creosote flats along the gently west sloping bajada. The elevation along this route ranged from 350 m at Maricopa to almost 450 m at the pass at the eastern edge of the Maricopa Mountains to 230 m at the west end (Gila Bend).

The starting point for surveys at the SVP site was McMicken Dam (12S, 364650 E, 3722833 N), an earthen dike situated along the northwest boundary of the greater Phoenix Metropolitan area. From the dike, the roadway route progresses initially west, along the northern edge of the White Tank Mountains, to a point approximately 20 km to the west, just east of the Hassayampa River flood plain, and then turns south for another 20 km to the northern boundary (12S, 344199 E, 3705479 N) of development associated with Interstate 10, and the recently expanded town of Buckeye, for a total survey route of 40 km. SVP was located primarily in Arizona Upland subdivision, characterized by Saguaro cactus, Ocotillo, Foothill Palo Verde, and Brittlebush, with Triangle-leaf Bursage and Creosote more numerous near the edge of the Hassayampa River floodplain in the Lower Colorado River Valley subdivision. The elevation along this route ranged from 410 m at McMicken Dam to almost 500 m at the edge of the Hassayampa flood plain, down to 350 m at the terminus of the survey area north of Interstate 10. The entire survey area was situated along the northern and western lower bajada or outflow skirt of the White Tank Mountains (Figs. 3, 5).

The roadways used as survey transects were the primary access routes for residents in the immediate vicinity for both regions, but they differed dramatically in a number of respects. During the initial survey period (1982–1998) MR-238 was a little used (< 500 vehicles per day; data available from Arizona Department of Transportation: http://www.mag.maricopa.gov), two-lane road with vegetation close to the roadway edge that

TABLE 1. Snakes encountered at the MR-238 (N = 397 snakes, 1982–2006) and Sun Valley Parkway (N = 175 snakes, 1998–2009) sites near Phoenix, Arizona, USA (listed in order of abundance at MR-238). Note: *Hypsiglena torquata* = *H. chlorophaea*.

Species	MR-238 Total (%)	SVP Total (%)
Crotalus cerastes	135 (34.0)	66 (37.7)
C. scutulatus	51 (12.9)	24 (13.7)
Rhinocheilus lecontei	47 (11.8)	18 (10.3)
C. atrox	32 (8.1)	15 (8.6)
Chionactis occipitalis	31 (7.8)	6 (3.4)
Phyllorhynchus decurtatus	23 (5.8)	2 (1.1)
Pituophis catenifer	20 (5.0)	12 (6.9)
Hypsiglena torquata	18 (4.5)	10 (5.7)
Arizona elegans	13 (3.3)	3 (1.7)
Masticophis flagellum	8 (2.0)	4 (2.3)
Lampropeltis getula	7 (1.8)	5 (2.9)
Leptotyphlops humilis	5 (1.3)	0 (0.0)
Salvadora hexalepis	2 (0.5)	8 (4.6)
Chilomeniscus cinctus	2 (0.5)	1 (0.6)
Thamnophis marcianus	2 (0.5)	0 (0.0)
Sonora semiannulata	1 (0.3)	0 (0.0)
Trimorphodon biscutatus	0 (0.0)	1 (0.6)

was initially unpaved, then paved for the easternmost 33 km in 1988. The final stretch of the roadway through the Maricopa Mountains and west to Gila Bend was paved late in 1999; the newly paved section was wider, with broad graded shoulders 3–5 m wide.

SVP, on the other hand, was also initially little used (1987–2002; < 500 vehicles per day; http://www.mag.maricopa.gov), but was a much larger roadway with two lanes and an emergency parking lane on either side of a vegetated median (2 m in width). Thus, the width of SVP was approximately three times that of MR-238. The area surrounding SVP was largely unpopulated in the 1980s and 1990s, though increasing traffic associated with construction and occupation of homes occurred after 2005. Extensive development (grading of the habitat on one side of the roadway, construction of side roads, etc.) was initiated along a 3 km stretch in the middle of the SVP study region in 2006.

Statistical methodology follows Zar (1999): we used chi-square tests to assess shifts in frequency, and Pearson's correlation coefficient was used to assess similarity in abundance across sites. We used SPSS (version 16.0, SPSS for Windows, Rel. 16.0.2., 15 November 2007, Chicago: SPSS Inc.) for all calculations and α = 0.05 for all tests.

RESULTS

Overall, we conducted 50 road-riding surveys at SVP, yielding 175 snakes in 2,538 km traveled for a net result of 0.069 snakes per km. All surveys reported here were conducted over the first 40 km of the SVP, with only a few km contained entirely within the Lower Colorado River Valley subdivision near the Hassayampa River (Figs. 3, 5). For MR-238, we conducted 80 road riding surveys, yielding 397 snakes in 6,391 km traveled for a net result of 0.062 snakes per km. Of the surveys at MR-238, 56% were entirely restricted to the Lower Colorado River Valley subdivision (0-33 km); 44% included roughly 10 km of Arizona Upland subdivision within the pass through the Maricopa Mountains, and an additional 22 km of Lower Colorado River Valley subdivision to the west of the Maricopa Mountains (toward Gila Bend).

***Similarities in community structure*.**—The two sites were largely similar in the diversity and abundance of snakes observed: we detected 17 species at the MR-238 site, and 14 of those were also found at the SVP site; a single species observed at SVP was not found at MR-238 (Table 1). Abundances of individual snake species (percentage of total) observed at the two sites were highly correlated (r = 0.97; $P < 0.001$).

Four species (*Crotalus cerastes, C. scutulatus, C. atrox*, and *Rhinocheilus lecontei*) accounted for 67% of the snakes observed at MR-238; these same four species were ranked one through four in abundance and accounted for 70% of the snakes observed at SVP (Table 1; note that for MR-238, *Chionactis occipitalis* was almost as abundant as *C. atrox*). The crotalids showed similar distributions at the two sites: *C. cerastes* and *C. scutulatus* were most numerous in the Creosote flats of the Lower Colorado River Valley subdivision at MR-238 (~ 75% of individuals of these species were found between kms 16 and 40; Fig. 4), and in the Creosote flats at SVP within the Lower Colorado River Valley subdivision along the edge of the Hassayampa River floodplain (8–16 km west of McMicken; ~ 50% of individuals of each species). At SVP, we found *C. atrox* primarily (~ 50% of individuals) within the first 8 km, where the road passed closest to the bajada along the northern edge of the White Tank Mountains (Fig. 5) in Arizona Upland subdivision, and none were observed 25 km beyond the starting point in primarily Lower Colorado River Valley subdivision along the Hassayampa River on the western edge of the survey area.

Most species were represented by relatively few individuals, and some were associated with particular habitats along the roadways. For example, we found *Trimorphodon biscutatus*, a rock dwelling snake, at the eastern edge of SVP where the road passes closest to the White Tank Mountains. We found *Thamnophis marcianus*, a snake unexpected in the Sonoran Desert except along watercourses, only at MR-238 near agricultural lands with ample water (canals, holding ponds, etc.); it was also noted within 500 m of the SVP starting point, east of McMicken Dam, where the road enters agricultural land. *Phyllorynchus decurtatus*, a snake often found in relatively open habitats of the driest of the North American deserts, was more abundant at the lower elevation MR-238 site and we only detected it twice at the SVP site near the Hassayampa River floodplain. Prior to the paving of the eastern portion of MR-238, we recorded neither *Chionactis* nor *Phyllorhynchus*, and only one *Hypsiglena*, suggesting that relative to a dirt roadway, detection of small forms was increased against the dark, smooth surface of the pavement.

Increased mortality of snakes.—Traffic volume increased significantly in association with the paving of the final section of MR-238 in 1999: daily traffic counts varied between 500 to roughly 1,000 vehicles for the 1980s and 1990s, but had increased to 4,000 vehicles/day by 2002 (data available from Arizona Department of Transportation: http://www.mag.maricopa.gov). The number of DOR snakes at MR-238 increased significantly following paving of the entire roadway in 1999. Specifically, from 1982 to 1987, when the roadway was unpaved, 20% of snakes we encountered DOR (16 DOR/66 AOR), but from 2000 to 2006, after the entire roadway was paved and traffic increased, 64% of snakes were DOR (88 DOR/50 AOR; $\chi^2 = 40.42$, df = 1, $P < 0.001$). To avoid contrasting an unpaved road with one that is entirely paved, we examined data from 1988-1999 (the eastern-most 33 km of the survey route was paved in this time period), in which 26% of snakes were DOR (48 DOR/134 AOR). This was also significantly less than the percentage of DOR individuals (64%) following the traffic increase in 2000 ($\chi^2 = 44.91$, df = 1, $P < 0.001$).

For SVP, traffic numbers increased dramatically around 2005, presumably associated with the higher volume of traffic in later years due to development. Prior to 2002, daily traffic volumes were under 500 vehicles/day, but by 2008, had reached 3,000 vehicles/day (Arizona Department of Transportation: http://www.mag.maricopa.gov). Although the total number of snakes declined with survey trips over time from 1998 through 2009 (107 snakes in the first 25 surveys; 68 snakes in the last 25 surveys), the percentage of DOR snakes (27 DOR/80 AOR = 25% DOR) for the first 25 survey nights (1998–2002) was roughly equivalent to the percentage of DOR snakes (20 DOR/48 AOR = 29% DOR) for the last 25 survey nights ($\chi^2 = 0.37$, df = 1, $P > 0.10$). However, an indication of reduced abundance (or avoidance of the roadway by individual snakes) was evidenced by the frequency of "snakeless" nights (surveys during which no snakes were detected) that was higher in the latter portion of the study: over the first 25 survey nights (1998–2002), there were no "snakeless" nights; however, over the last 25 survey nights, there were six nights that were snakeless ($\chi^2 = 6.42$, df = 1, $P < 0.01$).

Discussion

***Southwest snake communities*.—**Other investigations have used roadways to assess the diversity and abundance of snakes in Arizona, California, and New Mexico. Rosen and Lowe (1994) described the snake community of a fundamentally similar habitat, Arizona Upland subdivision Sonoran Desert, only 150 km to the southwest of the two sites we surveyed. In contrast to our results, they documented 20 species (368 individuals; 0.024 snakes per km) with *Crotalus atrox* as the most numerous and *Rhinocheilus lecontei* second, and *C. cerastes* was ranked ninth in relative abundance. They attributed the relatively low abundance of *C. cerastes* to the habitat they surveyed representing "middle bajada" (i.e., rockier, relatively upland habitat).

Our results indicate that in spite of differing proportions of Arizona Upland and Lower Colorado River Valley subdivision communities of the Sonoran Desert at SVP and MR-238, based on road-riding surveys, the snake communities are similar. It is perhaps even more surprising that road-riding methods in which different observers using vehicles with a variety of headlights, illuminating road surfaces of varying width and type, produced such similar results. All 17 species documented at MR-238 occur at the SVP site: the three taxa that were not observed in the course of surveys we conducted from 1998 through 2009 were detected on the roadway either by other collectors (*Sonora semiannulata* and *Leptotyphlops humilis*; Ryan Sawby and Erik Gergus, pers. comm.) or within a few hundred meters of the eastern boundary of the SVP site (*Thamnophis marcianus*) over the past decade (BKS, pers. obs.). Similarly, though not detected on the roadway at MR-238, *Trimorphodon biscutatus* (the only species we observed at SVP but not MR-238) is known

FIGURE 6. The four most common species at SVP and MR-238: *Crotalus cerastes* (upper left), *C. scutulatus* (upper right), *C. atrox* (lower left) and *Rhinocheilus lecontei* (lower right; all photographs by Randall Babb).

from the Maricopa Mountains adjacent to MR-238 (RDB, pers. obs.). Since the completion of our study, two additional species not previously recorded on MR-238 have been detected on the roadway: *Phyllorhynchus browni* (C. Akins and J. Pullins, pers. comm.), and *Micruroides euryxanthus* (TRJ, pers. obs.), suggesting extensive road sampling is necessary to document snake communities thoroughly. Nonetheless, at least on the basis of road-riding methods, the snake communities at SVP and MR-238 are similar in both diversity and abundance of species. It is especially striking that four of the same species (Fig. 6) were numerically dominant at both sites (although *Chionactis occipitalis* was virtually as common as *Crotalus atrox* at MR-238).

Mendelson and Jennings (1992) used road riding to survey two adjacent areas, one in a Chihuahuan Desert scrub habitat, and the other in a Plains Basin Grassland habitat, and for these communities they documented that *Crotalus atrox* and *C. scutulatus* were ranked either first, second, or third in relative abundance. These two species accounted for the majority of individual snakes they encountered, and they suggested that *C. atrox* had expanded at the expense of *C. scutulatus* since the early 1960s due to the conversion of grassland to desert scrub habitat as a result of over-grazing by cattle, and other anthropogenic activities in recent decades. Interestingly, Price and LaPointe (1990) used road riding as a survey technique and also documented that *C. atrox* was the numerically dominant snake in southcentral New Mexico, although *Pituophis catenifer* was second in abundance. Like Mendelsson and Jennings (1992), Price and LaPointe (1990) also found that *Rhinocheilus lecontei* ranked between 6th and 7th in relative abundance among the 18 species of snakes they observed.

In habitats that are more mesic, such as grassland and oak woodland/chaparral mosaics in California, road-riding surveys indicate *Pituophis catenifer* is by far the most abundant snake species (Klauber 1939; Sullivan 2000). In a road-riding survey of a Great Basin Desert scrub habitat in southern Idaho, Jochimsen (2006) also found that *P. catenifer* was the most common snake detected on paved roads even though off-road survey methods suggested *Crotalus oreganus* was the more common snake in the immediate vicinity. These results highlight the caution required in extending results from road-riding studies to estimation of the absolute abundance of snakes in the biotic communities adjacent to roadways. Nonetheless, given that *P. catenifer* appear especially likely to be found on roadways (Jochimsen 2006), our results and those of Rosen and Lowe (1994) suggest that this species does not numerically dominate the Sonoran Desert biotic communities as it does in either grassland (Sullivan 2000) or Chihuahuan Desert (Price and LaPointe 1990) habitats of the American Southwest.

Movement patterns and home range sizes determined in other studies of squamates of the American Southwest help explain distributional patterns of snake encounters at our study sites. For example, *Crotalus atrox* in the Sonoran Desert near Tucson made predictable movements from rocky upland habitats to creosote flats each year (Beck 1995). Our observations at SVP are consistent with Beck's findings in that the majority of individuals of this species at SVP were observed within the first half of the transect along the bajada: snakes moving from rocky upland sites would be forced to cross the road to move down slope toward the creosote flats. In sand dune habitats of the Mojave Desert of California, *C. cerastes* exhibit large home ranges (~ 25 ha) relative to even much larger snakes (Secor 1994). Home ranges of *C. cerastes* studied by Secor (1994) are roughly five times as large as those of *C. atrox* reported by Beck (1995) approximately 150 km southeast of our sites. Similarly, Cardwell (2008) documented that male *C. scutulatus* in the Mojave Desert of California exhibit a home range as large as *C. cerastes*, whereas females have a smaller home range similar in size to *C. atrox*. *Crotalus cerastes* is a sit-and-wait predator (Secor 1994), and as such would not be expected to be numerically dominant on roadways at both of our sites (Bonnett et al. 1999). The large numbers we observed at SVP and MR-238 in part could be due to these snakes, as well as male *C. scutulatus*, making relatively larger movements in search of prey ambush sites, mates or refuges within their respective home ranges.

***Increased mortality of snakes*.—**Declines in numbers of snakes observed (SVP), or in the number of AOR individuals detected (MR-238), were correlated with dramatic increases in roadway traffic volume. The increase in traffic volumes from ~ 500 vehicles per day to over 3,000 vehicles per day at both of our sites was coincident with a decline in AOR snakes, a finding surprisingly similar to results obtained by Sutherland et al. (2010) in a road-riding study of amphibians in North Carolina in relation to traffic volume. Their analyses indicated that almost twenty times as many amphibians were found on roads with < 550 vehicles per day than the number found on roads with > 2,000 vehicles per day.

Coleman et al. (2008) documented higher numbers of DOR reptiles with increasing vehicular use of the roadways. They also reported seasonal shifts in numbers of DOR reptiles, with higher numbers during the spring and fall activity periods (see also Reynolds 1982). Studies of *Elaphe obsoleta* (Row et al. 2007), *Sistrurus catenatus* (Shepard et al. 2008), and *Drymarchon couperi* (Hyslop et al. 2009) suggest that roadway mortality can significantly affect viability of small populations of threatened or endangered snakes. It is increasingly clear that roadway traffic is a significant contributor to the mortality of snakes because they not only cross roads when moving among habitat patches, but may actively use paved roads to thermoregulate under appropriate thermal conditions (Sullivan 1981b).

Behavioral observations of *Thamnophis sirtalis* indicate that they avoid roads, and cross in the most direct path if necessary (Shine et al. 2004), and Andrews and Gibbons (2005, 2006) reported that smaller species of snakes were less likely than larger species to cross roads. Hensley (1950) and Jochimsen (2006) detected a male bias in the sex ratio of DOR snakes observed on roads, presumably because males move long distances when searching for mates during the breeding season (Sullivan in press), and are thus expected to be disproportionately represented in road surveys. If some snake species avoid roads more than others, then such behavior may confound the use of road riding as a means to assess the population biology of snakes or their response to anthropogenic activities. If roadway surveys are used to estimate mortality effects at the population level, it is also important to recognize that scavengers (e.g., ravens [*Corvus* spp.], Turkey Vultures [*Cathartes aura*], Coyotes [*Canis latrans*]) systematically patrol paved roads in the American Southwest searching for carrion (Sullivan 2000; Antworth et al. 2005). The lack of an increase in the number of DOR snakes detected at SVP in latter survey years may be attributable to the size of the roadway (width) and the prospect of both other collectors and scavengers removing dead snakes. It may be that the number of DOR specimens recorded in a road riding survey dramatically underestimates mortality for local snake populations.

Heavily used roadways impact the ecology not only of snakes, but also the entire biotic community adjacent to the roadway (Jochimsen 2006). Roadways alter the hydrology, chemistry, physical structure, and other properties of habitats in many ways (e.g., Garland and Bradley 1984; Artz 1989; Terranella et al. 1999). Roadways lead to the deaths of snakes and other organisms, including their prey, and presumably affect the population biology of many taxa within the local biotic community (Fahrig et al. 1994; Spellerberg 1998; Trombulak and Frissell 2000). Overall, it is reasonable to infer that reptile communities in the immediate vicinity of roadways will be altered over time depending in part on traffic volumes and other local variables (Bernardino and Dalrymple 1992; Spellerberg 1998; Garcia et al. 2007). Clark et al. (2010) recently documented that roadways can significantly impact the genetic structure of crotalid populations, underscoring the potential consequences of these anthropogenic barriers to movement patterns of snakes; they noted that more heavily traveled roads exacerbated these genetic effects.

Sullivan (1981a, 2000), like Mendelson and Jennings (1992), noted a shift in community structure over 20 years using road riding to survey distribution and abundance of snakes across an ecotone in central California. Because Sullivan (2000) conducted his surveys in two periods that differed dramatically in precipitation (resurvey years were much higher in rainfall), he could not determine if the change in relative abundance of the two most common snakes was due to anthropogenic changes along the roadway over time, or simply a differential response to rainfall in one species in the resurvey period. Even if road-riding surveys are conducted by the same personnel at the same site, variation in abiotic conditions may lead to shifts unrelated to roadway effects. As noted by Jochimsen (2006), it remains for future investigators to document more fully the impact of roadways on snake communities through both road riding and other survey methods assessing the nature of community effects well away from survey routes. It will also be important to assess the influence of climate change on snake communities, especially those in the vicinity of urban regions that experience not only increasing traffic volumes, but heat island effects, off-road vehicle recreational activities and a host of anthropogenic disturbances.

Acknowledgments.—J. Kevin Aitkin, Robert Bowker, Christina Akins, Thomas Brennan, Lisa Bucci, William Burger, Brian Carr, Ken Crawford, Chris Cuciti, Teal Richards Dimitrie, Marty Feldner, Philip Fernandez, Krista Fish, Erik Gergus, H. Carl Gerhardt, Matthew Grober, Paul S. Hamilton, Robert Hegna, Adele Hensley, Paul Hershberger, Andrew Holycross, April Jones, Carol Kissler, Jamie Kruse-Hall, Matthew Kwiatkowski, Barry Mansell, Johan Marais, Peter Mayne, Brian McGuire, Paul Moler, Jamie Myers, Lewis Obermiller, Audrey Owens, Justin Pullins, Tansey Pullins, Sheri Reeves, J. Dale Roberts, Ryan Sawby, Gordon Schuett, Angela Schwendiman, Richard Seigel, Michael Sredl, Justin, Kyle and Tom Stoneking, Daniel, Elizabeth, Justin and Keith Sullivan, Ross Timmons, Sally Weimann, Kim Wismann, and Michael Worrell assisted with some field observations. We thank Matthew Kwiatkowski for comments on a previous draft of the manuscript, and Joyce Francis for preparing Fig. 3. All research was permitted by the Arizona Game and Fish Department and ASU IACUC approval.

LITERATURE CITED

Andrews, K.M., and J.W. Gibbons. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 2005:772–782.

Andrews, K.M., and J.W. Gibbons. 2006. Dissimilarities in behavioral responses of snakes to roads and vehicles have implications for differential impacts across species. Pp. 339–350 *In* Proceedings of the 2005 International Conference on Ecology and Transportation. Irwin, C.L., P. Garrett, and K.P. McDermott (Eds.). Center for Transportation and the Environment, North Carolina State University, Raleigh, North Carolina, USA.

Antworth, R.L., D.A. Pike, and E.E. Stevens. 2005. Hit and run: effects of scavenging on estimates of roadkilled vertebrates. Southeastern Naturalist 4:647–656.

Artz, M.C. 1989. Impacts of corridors on perennial vegetation in the east Mojave Desert: Implications for environmental management and planning. Natural Areas Journal 9:117–129.

Beck, D.D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. Journal of Herpetology 29:211–223.

Bernardino, F.S., and G.H. Dalrymple. 1992. Seasonal activity and road mortality of the snakes of the Pa-hay-okee wetands of Everglades National Park, USA. Biological Conservation 62:71–75.

Bonnett, X., G. Naulleau, and R. Shine. 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89:39–50.

Bugbee, R.E. 1945. A note on the mortality of snakes on highways in western Kansas. Transactions Kansas Academy of Science 47:373–374.

Cardwell, M.D. 2008. The reproductive ecology of Mohave rattlesnakes. Journal of Zoology 274:65–76.

Clark, R.W., W.S. Brown, R. Stechert, and K.R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in Timber Rattlesnakes. Conservation Biology 24:1059–1069.

Coleman, J.L., N.B. Ford, and K. Herriman. 2008. A road survey of amphibians and reptiles in a bottomland hardwood forest. Southeastern Naturalist 7:339–348.

Dodd, C.K., K.M. Enge, and J.N. Stuart. 1989. Reptiles on highways in north-central Alabama, USA. Journal of Herpetology 23:197–200.

Fahrig, L., J.H. Pedlar, S.E. Pope, P.D. Taylor, and J.F. Wegner. 1994. Effect of road traffic on amphibian density. Biological Conservation 73:177–182.

Garcia, J.D.D., J.R. Arevalo, and J.M. Fernandez-Palacios. 2007. Road edge effect on abundance of the lizard *Gallotia galloti* (Sauria: Lacertidae) in two Canary Island forests. Biodiveristy and Conservation 16:2949–2963.

Garland, T., and G. Bradley. 1984. Effects of a highway on Mojave Desert rodent populations. American Midland Naturalist 111:47–56.

Hensley, M.M. 1950. Results of a herpetological reconnaissance in extreme southwestern Arizona and adjacent Sonora, with a description of a new subspecies of the Sonoran Whipsnake (*Masticophis bilineatus*). Transactions Kansas Academy of Science 53:270–288.

Hyslop, N.L., J.M. Meyers, R.J. Cooper, and T.M. Norton. 2009. Survival of radio-implanted *Drymarchon couperi* (Eastern Indigo Snake) in relation to body size and sex. Herpetologica 65:199–206.

Jochimsen, D.M. 2006. Factors influencing the road mortality of snakes on the Upper Snake River Plain, Idaho. Pp. 351–365 *In* Proceedings of the 2005 International Conference on Ecology and Transportation. Irwin, C.L., P. Garrett, and K.P. McDermott (Eds.). Center for Transportation and the Environment, North Carolina State University, Raleigh, North Carolina, USA.

Klauber, L.M. 1939. Studies of reptile life in the arid southwest. Bulletin of the Zoological Society of San Diego 14:1–100.

Kjoss, V.A., and J.A. Litvaitis. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation 98:285–292.

Langen, T.A., A. Machniak, E.K. Crowe, C. Mangan, D.F. Marker, N. Liddle, and B. Roden. 2007. Methodologies for surveying herpetofauna mortality on rural highways. Journal of Wildlife Management 71:1361–1368.

Luiselli, F. 2007. Community ecology of African reptiles: historical perspective and a meta-analysis using null models. African Journal Science 46:384–394.

Mendelson, J.R., and W.B. Jennings. 1992. Shifts in the relative abundance of snakes in a desert grassland. Journal of Herpetology 26:38–45.

Pianka, E.R. 1986. Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton, New Jersey, USA.

Pough, F.H. 1966. Ecological relationships of rattlesnakes in southeastern Arizona with notes on other species. Copeia 1966:676–683.

Price, A.H., and J.L. LaPointe. 1990. Activity patterns of a Chihuahuan desert snake community. Annals of Carnegie Museum 59:15–23.

Reynolds, R.P. 1982. Seasonal incidence of snakes in northeastern Chihuahua, Mexico. Southwestern Naturalist 27:161–166.

Rosen, P.C., and C.H. Lowe. 1994. Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biological Conservation 68:143–148.

Row, J.R., G. Blouin-Demers, and P.J. Weatherhead. 2007. Demographic effects of road mortality in Black Ratsnakes (*Elaphe obsoleta*). Biological Conservation 137:117–124.

Secor, S.M. 1994. Ecological significance of movements and activity range for the Sidewinder, *Crotalus cerastes*. Copeia 1994:631–645.

Shepard, D.B., M.J. Dreslik, B.C. Jellen, and C.A. Phillips. 2008. Reptile road mortality around an oasis in the Illinois corn desert with emphasis on the endangered Eastern Massasauga. Copeia 2008:350–359.

Shine, R., M. Lemaster, M. Wall, T. Langkilde, and R. Mason. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). Ecology and Society 9:1–13.

Spellerberg, I.F. 1998. Ecological effects of roads and traffic: A literature review. Global Ecology and Biogeography Letters 7:317–333.

Sullivan, B.K. 1981a. Distribution and relative abundance of snakes along a transect in California. Journal of Herpetology 15:247–248.

Sullivan, B.K. 1981b. Observed differences in body temperature and associated behavior of four snake species. Journal of Herpetology 15:245–246.

Sullivan, B.K. 2000. Long-term shifts in snake populations: A California site revisited. Biological Conservation 94:321–325.

Sullivan, B. K. In press. Road riding. *In* Measuring and Monitoring Biological Diversity: Standard Methods for Reptiles. Foster, M., R. McDiarmid, W. Gibbons (Eds.). U.C. Press, Berkeley, California, USA.

Sullivan, B.K., D.R. van Haverbeke, and C. Chambers. In press. Wildlife and anthropogenic changes in the arid southwest. *In* Design With the Desert. Malloy, R (Ed.). University of Arizona Press, Tucson, Arizona, USA.

Sutherland, R.W., P.R. Dunning, and W.M. Baker. 2010. Amphibian encounter rates on roads with different amounts of traffic and urbanization. Conservation Biology 24:1625–1635.

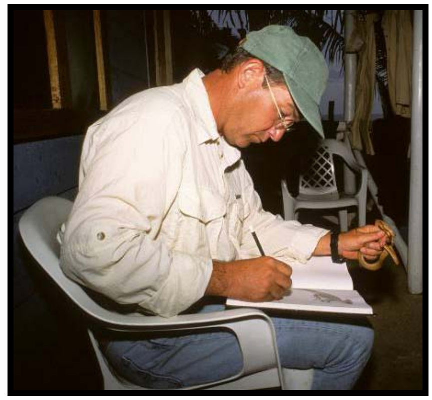
Terranella, A.C., L. Ganz, and J.J. Ebersole. 1999. Western Harvester Ants prefer nest sites near roads and trails. Southwestern Naturalist 44:382–384.

Trombulak, S.C., and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

Turner, R.M., and D.E. Brown. 1982. Sonoran desertscrub. *In* Biotic communities of the American Southwest, United States and Mexico. Brown, D.E. (Ed.). Desert Plants 4:181–221.

Zar, J.H. 1999. Biostatistical Analysis. 4th edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

TOM JONES is the Amphibians and Reptiles Program Manager for the Arizona Game and Fish Department where he oversees conservation and management of amphibians and reptiles in Arizona. For 11 years he was on the faculty of Grand Canyon University before coming to the Arizona Game and Fish Department in 2005. Research interests include ecology and population and conservation biology of amphibians and reptiles. He has done field work in much of the continental United States, and in México, Panamá, Costa Rica, and Vietnam. (Photographed by Joe Kolb)



RANDY BABB is a biologist employed by the Arizona Game and Fish Department where he works out of the Mesa Regional Office as the Information and Education Program Manager. His interests range from small mammals and invertebrates to reptiles and amphibians. He has participated in numerous studies and projects in Arizona, New Mexico, the southeastern U.S., México, Central America, Vietnam, and southern Africa. (Photographed by Thomas R. Jones)

FRANK R. HENSLEY is Associate Professor of Biology at Trinity Christian College in Palos Heights, Illinois. His primary research interest is the ecology and conservation of vertebrates that are difficult to study due to low population density or cryptic habits. His current studies include spatial ecology of brownsnakes (*Storeria* sp.) and phenology and behavior of bats in response to seasons and weather patterns. (Photographed by Frank R. Hensley)

CHRISTINE LIWANPO is a medical student at Midwestern University in Glendale, Arizona. During her undergraduate studies she participated in a variety of ecological research projects including studies of the demography and spatial ecology of various reptiles and arachnids. Although she is pursuing a career in medicine, she is a dedicated nature photographer who has photographed wildlife in Costa Rica, Mauritius, and her native Ontario. (Photographed by Thomas R. Jones)

BRIAN SULLIVAN has been a Full Professor at Arizona State University since 2002, and served as the Editor of the *Journal of Herpetology* from 2000 through 2005. He is currently investigating acoustic communication in desert amphibians, temporal and spatial dynamics of hybridization between Arizona (*Bufo microscaphus*) and Woodhouse's (*B. woodhousii*) toads in the Southwest, the nature of species boundaries among toads and lizards, and anthropogenic impacts on amphibians and reptiles of arid regions. (Photographed by Elizabeth Sullivan).