

Sharing the Resource: Six Species of Rattlesnakes in Joshua Tree National Park, California

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Photographs by the author except where noted.

The competitive exclusion principle would seem to apply to six species of rattlesnakes in the genus *Crotalus*, all of which feed mostly on small mammals. In Joshua Tree National Park, California, however, six species occur in an area of just 400,000 ha. A pattern noted in ecology is that diversity at one level begets diversity at other levels. Almost 70 years of locality data combined with present field research was used as evidence for the hypothesis that these rattlesnake species mostly avoid competitive exclusion by microhabitat differences within the great diversity of ecological communities in the park. These long-term records might also indicate that the dynamics of the desert ecosystem could be changing, possibly the result of climate change and/or local urbanization.

Introduction

Ecological theory predicts that species in ecological communities can coexist only if they differ in their responses to limiting resources. This competitive exclusion principle would seem to apply to the six species of rattlesnakes in the single genus *Crotalus* in the area (400,000 ha) of Joshua Tree National Park (JTNP). Adult rattlesnakes feed almost exclusively on small mammals (Mackessy 1988, Beavers 1976), with the exception of Sidewinders (*C. cerastes*), for which mammals comprise about 50% of the diet (Funk 1965). In JTNP, the ubiquitous Merriam's Kangaroo Rat (*Dipodomys merriami*) probably makes up the bulk of the diet of all six species, as it does elsewhere in the desert (Reynolds and Scott 1982), whereas Side-blotched Lizards (*Uta stansburiana*) almost certainly serve the same role for hatchling rattlesnakes. How does this limited resource support so many closely related species without violating ecological theory?

Materials and Methods

Joshua Tree National Park is an ideal place to study rattlesnake ecology. Its protected status has preserved natural habitats in fairly good condition for 70 years. The first herpetological survey of what was then a national monument was conducted by Robert C. Stebbins from 1945–1955. R.B. Loomis and his colleagues continued to inventory the reptiles during the 1960s. I began periodic herpetological visits to the Park in the 1970s, and conducted season-long (March–November) surveys in 1999–2005. In addition, observation records made by rangers and others have been accumulating for almost 50 years. The result (Table 1) is that we have accumulated some 400 locality data reports on Western Diamondback Rattlesnakes (*C. atrox*; 18), Southern Pacific Rattlesnakes (*C. helleri*; 60), Red Diamond Rattlesnakes (*C. ruber*; 15), Mojave Rattlesnakes (*C. scutulatus*; 21), Southwestern Speckled Rattlesnakes (*C. pyrrhus*; 155), and Sidewinders (*C. cerastes*; 133).

All locality data were plotted on a map of the park using ESRI ArcView. These species maps were then compared with maps showing vegetation patterns (Leary 1977). Extensive fieldwork was conducted in areas of sympatry to identify possible differences in microhabitats within Leary's habitat (vegetation association) types. These data were used to test the hypothesis that the rattlesnakes in the park avoid competitive exclusion primarily by partitioning microhabitats.

Multivariate analyses of habitats were not employed, but work elsewhere (Reinert 1984a, 1984b) indicated that habitat separation is probably

the chief method for snakes that prey on small mammals to avoid niche competition. Because "habitat" is a very broad category that can include a



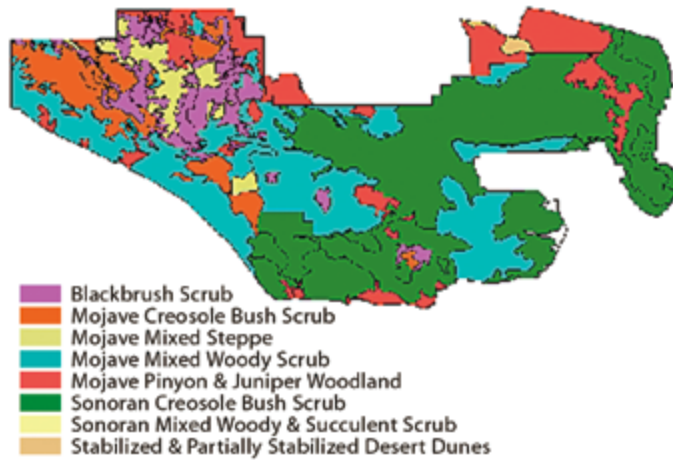
PHOTOGRAPH COURTESY OF NATIONAL PARK SERVICE



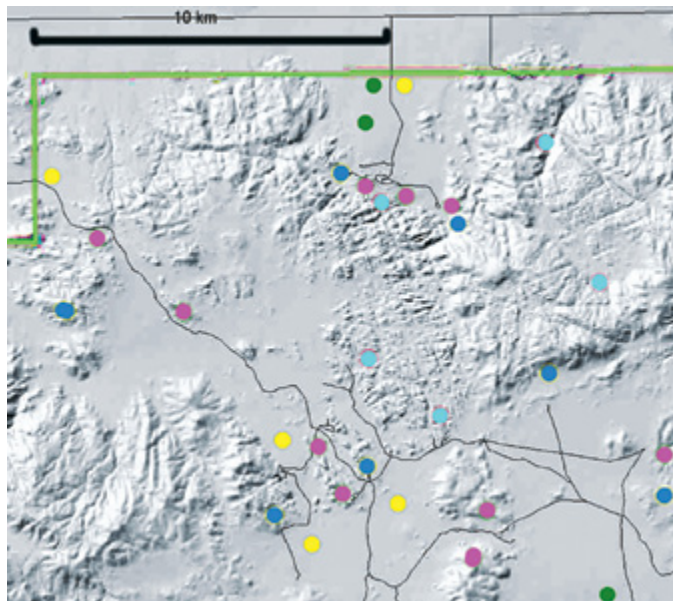
The ubiquitous Merriam's Kangaroo Rat (*Dipodomys merriami*) is taken by larger rattlesnakes of all species, whereas hatchlings feed largely on the phenomenally abundant Side-blotched Lizards (*Uta stansburiana*).



Location of Joshua Tree National Park and local ecoregions (the small square indicates the Indian Cove area).



The ecological communities in Joshua Tree National Park.



The Indian Cove area, with locality records for *Crotalus cerastes* (green), *C. helleri* (dark blue), *C. pyrrhus* (magenta), *C. ruber* (light blue), and *C. scutulatus* (yellow).



Western Diamondback Rattlesnakes (*Crotalus atrox*) are confined mostly to the Sonoran Desert ecoregion.



Sidewinders (*Crotalus cerastes*) appear to be limited to areas with sandy substrates.

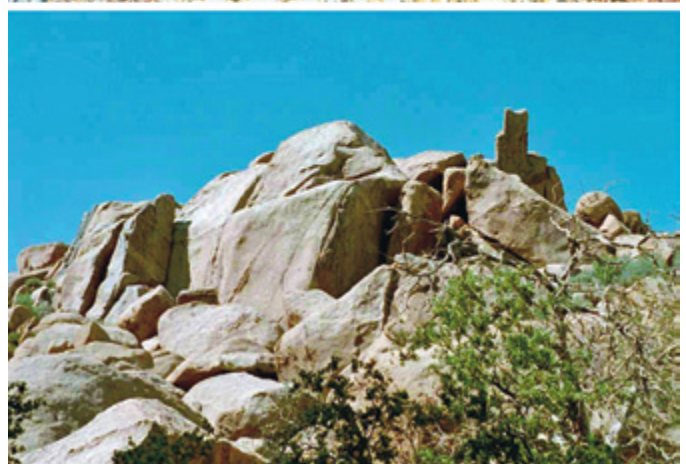


Southern Pacific Rattlesnakes (*Crotalus helleri*) inhabit rocky areas within the Pinyon-Juniper community.

variety of dissimilar entities, approaching the concept from a snake's perspective, rather than our own, is important. Every individual has to: (1) Get to a place (or be born there), (2) be able to exploit all essential resources, and (3) avoid deleterious conditions, which might be episodic but can be severe. These factors are distributed on several scales, from <1m to many km².



PHOTOGRAPH COURTESY OF NATIONAL PARK SERVICE



Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) occur in rocky canyons, hills, and ridges in the eastern half of the park, but appear to be limited to rocky canyons in the western half.

Red Diamond Rattlesnakes (*Crotalus ruber*) occur in the southwestern corner of the park and an isolated population is known from the Wonderland of Rocks.

Results

Crotalus atrox reaches the northern-most point of its distribution in California within JTNP. It is mostly confined to the Sonoran Desert ecoregion section. *Crotalus cerastes* seems strictly limited to areas of sand substrate. *Crotalus scutulatus* reaches the southern-most extent of its range in California in the northwestern part of JTNP. It appears limited in occurrence to Joshua Tree flats. *Crotalus helleri* inhabits rocky areas within the Pinyon-Juniper community. All locality records are within areas with California Junipers (*Juniperus californicus*). *Crotalus ruber* occurs in two apparently disjunct populations in JTNP. One, in the southwestern corner of the park, is probably the eastern terminus of the main population of the desert foothills (e.g., Whitewater Canyon). The second has long been con-

sidered an isolated population within the Wonderland of Rocks, where it is associated with large outcroppings of monzogranite in very rugged terrain. *Crotalus pyrrhus* is the most abundant species of rattlesnake in JTNP. In the eastern half of the park, it is the only species occurring in rocky canyons, hills, and ridges. In the western half of the park it seems to have a narrower niche, and appears to be limited to rocky canyons. It does occur to elevations as high as 1,525 m above sea level.

Most species were clearly associated with particular habitat types. However, the locality data revealed one area of the park in which five species of *Crotalus* (*cerastes*, *ruber*, *helleri*, *pyrrhus*, *scutulatus*) appear to be sympatric. This area centers around Indian Cove. Ground reconnaissance of the localities of sympatry revealed that the species are not syntopic.

Table 1. Basic habitat types and locality records by species.

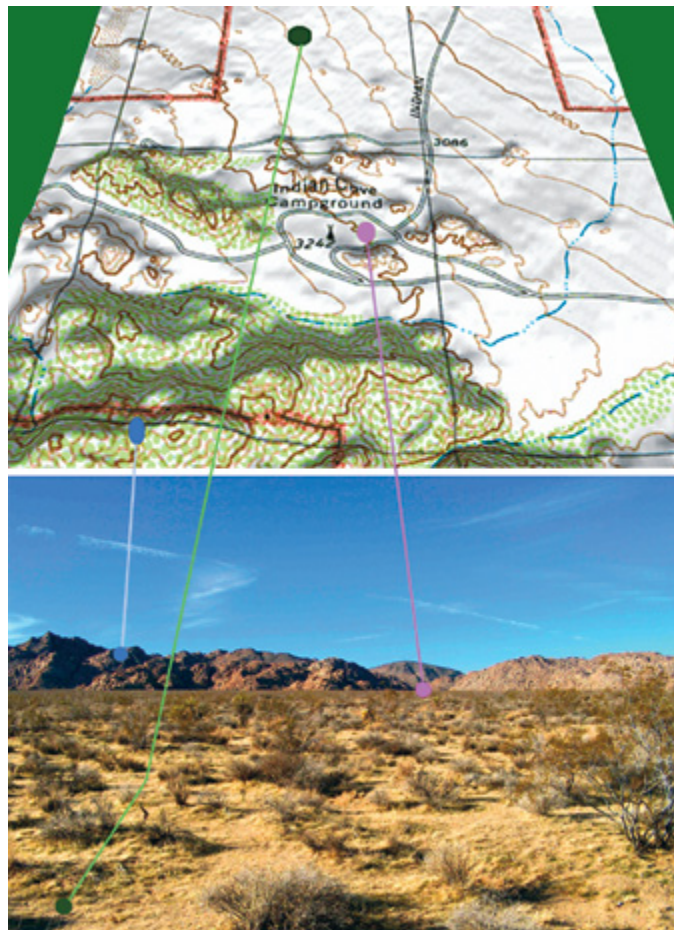
Habitat Types	Species of <i>Crotalus</i>					
	<i>C. atrox</i>	<i>C. cerastes</i>	<i>C. helleri</i>	<i>C. pyrrhus</i>	<i>C. ruber</i>	<i>C. scutulatus</i>
Rocky canyons W	20		19	45	10	14
Rocky canyons E	80			31		
Rocky ridges W (pinyon-juniper)				81	4	90
Rocky ridges E				1		
Joshua flats W				11		86
Creosote flats E				8		
Sandy washes/flats W		10				
Sandy washes/flats E		90				



Mojave Rattlesnakes (*Crotalus scutulatus*) reach the southern-most extent of their range in California in the northwestern part of JTNP. The species appears to be limited in occurrence to Joshua Tree flats.

Discussion

Resources potentially subject to interspecific competition are food, place, and time. Locality records and field studies seem to support the hypothesis that niches are distinct at the microhabitat level. For the rattlesnakes of JTNP, shelter is probably in more than adequate supply, with holes and crevices essentially everywhere. Nocturnal-diurnal behavior is dictated by



The Indian Cove area, with the topographic map (top) and photograph showing the same view. Blue dots indicate habitat of *Crotalus helleri*, green dots that of *C. cerastes*, and magenta dots that of *C. pyrrhus*.

seasonal temperatures and appears to be the same for all species at the same altitude. Very few quantitative studies of the diets of rattlesnakes have been conducted. The few existing dietary data for these species were determined elsewhere in their range. That they are essentially the same in JTNP may or may not be a valid assumption, as dietary shifts are known to occur in wide-ranging species.

The rattlesnake distribution in the park may be changing along with ecosystem changes. The last verified sighting in the park of *C. scutulatus* was in 1991 (Keys Ranch). The two flatland corridors that lead from the north (main range of the Mojave Rattlesnake) are now largely blocked by urbanization. If the park was formerly a “sink” for movements of this species, the corridors are now mostly blocked, and the species may have become extirpated from the park, although it remains abundant 25 km to the north, on the other side of the urban development.

In the last two decades exotic grasses (mostly Cheat Grasses, *Bromus* spp.) have invaded much of the Juniper and Joshua Tree woodlands. These exotics have provided fuel for recurring wildfires in plant communities not adapted to fire. An intensive survey after the May 1999 fire showed that most reptiles survived the fire, but a subsequent survey during the following spring indicated a near total absence of all species in the burned area.

Acknowledgements

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