HABITAT USE, SPATIAL ECOLOGY, AND MANAGEMENT OF Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) in the Tinajas Altas Mountains of Yuma County, Arizona, USA

Ashley A. Grimsley-Padron^{1,5,7}, Austin B. Smith^{2,6}, Linden A. Piest³, Michael F. Ingraldi¹, and Thomas R. Jones⁴

¹Wildlife Contracts Branch, Arizona Game and Fish Department, 5000 West Carefree Highway, Phoenix, Arizona 85086, USA

²Information Systems Branch, Arizona Game and Fish Department, 5000 West Carefree Highway, Phoenix, Arizona 85086, USA

³Region 4, Arizona Game and Fish Department, 9140 28th Street, Yuma, Arizona 85365, USA ⁴Terrestrial Wildlife Branch, Arizona Game & Fish Department, 5000 West Carefree Highway, Phoenix, Arizona 85086, USA

⁵Current address: Wildlife Management Division, Arkansas Game and Fish Commission, 3400 North 40th Street, Springdale, Arkansas 72762, USA ⁶Current address: Haub School of Environment and Natural Resources, University of Wyoming,

804 East Fremont Street, Laramie, Wyoming 82072, USA

⁷Corresponding author; e-mail: agrimsley7@gmail.com

Abstract.—Illegal hunting and wildlife trafficking is a growing and prominent threat to species worldwide. An isolated population of Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) occurs in the Tinajas Altas Mountains of Yuma County, Arizona, USA. Individuals in this population are sought after in the pet trade because of their unique white-cream coloration. The ecology of this population is not well understood. We used telemetry to study habitat use, home range size, and movement patterns of 19 *C. pyrrhus* in this population from October 2017 to May 2019. We calculated home ranges with both Minimum Convex Polygons and Kernel Density Estimates. We most often found snakes on slopes (65%) using boulders as their primary cover (57%). We commonly observed snakes using Elephant Tree (*Bursera microphylla*) and Catclaw Acacia (*Senegalia greggii*) as vegetation cover, with low visibility for most observations. We observed annual variation in use of habitat type and daily variation in both cover type and visibility. Minimum Convex Polygon estimates ranged from 0.91–13.74 ha. We found no significant difference in movements, activity areas, or core areas between males and females or between a near-average and an unusually wet winter season. This study provides novel habitat and spatial ecological information for guiding the management and conservation practices of this distinct population of *C. pyrhus*.

Key Words.-activity patterns; desert; home range; telemetry; Viperidae

INTRODUCTION

Illegal hunting and wildlife trafficking, occurring with alarming and increasing frequency, have had a negative impact on wildlife worldwide (Muth and Bowe 1998; Wyatt and Cao 2015; Rizzolo 2021). The extent of this pressure on wild populations, however, is currently unknown for many species. Approximately 53% of traded reptiles, and 97.8% of viperid snakes specifically, are wild-sourced (Hierink et al. 2020; Marshall et al. 2020). Many reptile species lack conservation assessments, with little to no population data. If reptiles are sourced from the wild, the viability of their populations could be at risk (Hierink et al. 2020; Marshall et al. 2020). Here, we address the management of a unique population of Southwestern Speckled Rattlesnake (*Crotalus pyrrhus*) in extreme southwestern Arizona. Primarily desert dwellers, *C. pyrrhus*, are widely distributed in the southwestern U.S., northern Baja California Peninsula, and northwestern Sonora, Mexico (McCrystal and McCoid 1986; Meik and Babb 2020). One of the most variable rattlesnakes in color and pattern across their range, *C. pyrrhus* varies from grayish-blue, brown, orange, or salmon to cream color, depending on locality (Klauber 1936, 1972), and this makes them prime targets of reptile dealers.

The remote, isolated population of *C. pyrrhus* in the Tinajas Altas Mountains (TAs), Yuma County, Arizona, USA, is known for its unusually light color



FIGURE 1. A Southwestern Speckled Rattlesnake (*Crotalus pyrrhus*) in the Tinajas Altas Mountains, Yuma County, Arizona, USA. (Photographed by Ashley A. Grimsley-Padron).

pattern not found elsewhere in the distribution of the species (Klauber 1936; 1972). The snakes have a cream-white color with black specks, matching the light-colored granite of the mountain (Meik 2016; Fig. 1). Because of their unique color pattern, snakes from this population are highly sought after by collectors and are legally and illegally taken from the wild (Michael Sumner, pers. comm.). The extent and possible effects of collecting individuals from this population are of conservation concern, and therefore, this population is considered a Species of Greatest Conservation Need in the Arizona State Wildlife Action Plan (Arizona Game and Fish Department 2022). The TAs are located on a U.S. Department of Defense (DOD) military installation. Current DOD management practices to conserve wildlife include law enforcement (i.e., U.S. Conservation Law Enforcement Officers [range wardens] and Arizona Game and Fish Department Wildlife Managers) and recreational range permit requirements.

Although we know collecting pressure has been exerted on this population, the effects of that pressure are not known. Jones and Goode (2020) described how commercialization and over-collecting of snakes may negatively affect populations; however, there are little data to suggest legal collecting has had an exceptionally negative effect on snakes at the species level in Arizona. Indeed, it is a complicated subject but it may depend on how many and which individuals are collected in this population. *Crotalus pyrrhus* has low fecundity, with a mean litter size of 5.8 (Klauber 1972; Goldberg 2000), and is one of few rattlesnake species that only mates in the spring (Goldberg 2000; Meik and Babb 2020). Consequently, collecting pressure that results in removing one or more of a

few breeding females could be detrimental to local populations. The ecology and population status of *C. pyrrhus* in the TAs would benefit from learning more about their habitat use and spatial ecology, which will help inform management and conservation practices.

Telemetry is an effective tool to assess habitat use, movements, and home ranges of rattlesnakes while providing data on the effects of factors such as seasonal and daily activity, weather, and sex on these measures (e.g., Beck 1995; Goode et al. 2008; Petersen et al. 2019). Although telemetry has become prevalent in rattlesnake research, there have been few spatial ecology studies of C. pyrrhus (e.g., Greenberg and McClintock 2008; Glaudas and Rodríguez-Robles 2011). Our primary objectives were to: (1) evaluate habitat use; (2) estimate home range sizes; and (3) evaluate movement patterns of C. pyrrhus in the TAs. Further, a goal of this project was to evaluate the ecology of the population to help determine susceptibility to illegal hunting and wildlife trafficking and provide a foundation of C. pyrrhus ecology for future management planning. These data will allow us to learn more about how individuals in this population use their habitat and infer how much habitat may be necessary to maintain stable populations. Our work advances our understanding of C. pyrrhus habitat use and spatial ecology and forms the first steps toward informing the management and conservation of this unique population.

MATERIALS AND METHODS

Study site.—We studied C. pyrrhus in the Tinajas Altas Mountains, Yuma County, Arizona, USA, in the Barry M. Goldwater Range-West (BMGR), a DOD installation managed by the U.S. Marine Corps (Fig. 2). This installation is in the Lower Colorado River Valley subdivision of the Sonoran Desert (Turner and Brown 1982). The BMGR is managed under the guidance of an Integrated Natural Resources Management Plan (Center for Environmental Management of Military Lands [CEMML] 2018) endorsed in partnership among the U.S. Marine Corps, U.S. Air Force, U.S. Fish and Wildlife Service, and the Arizona Game and Fish Department (AZGFD). The public can access several areas within the BMGR by obtaining a permit (https://bmgr.recaccess.com). These mountains are characterized by arid, hot summers, with mean daily highs of 41.4° C in July, and cooler winters, with mean daily lows of 6.8° C in January (Felger et al. 2012). Annual rainfall varies



FIGURE 2. Map of the study site for Southwestern Speckled Rattlesnake (*Crotalus pyrrhus*) telemetry conducted on the Barry M. Goldwater Range-West in the Tinajas Altas Mountains, Yuma County, Arizona, USA.

from 7.6 to 10.2 cm and occurs in a bimodal pattern (i.e., December to March and July to September; Felger et al. 2012). The terrain is mainly composed of light-colored granite, characterized by steep slopes with rugged canyons, and elevations range from 291 to 834 m, with an average of 425 m (Felger et al. 2012; Fig. 3). Our study site was in an area that appeared to have some of the highest levels of pressure by snake collectors within the Tinajas Altas Mountains, based on observations by biologists, range wardens, and AZGFD Wildlife Managers (Michael Sumner, pers. comm.). Additionally, *C. pyrrhus* in our study site was part of an ongoing mark-recapture project started in 2015 and led by BMGR and AZGFD.

Snake capture and processing.-We conducted visual searches for C. pyrrhus in the northern portion of the TAs in October 2017, November 2018, and early March 2019, primarily in the mornings and Upon detection, we captured snakes, evenings. recorded their location (UTM, datum NAD83), and temporarily flagged the site to return snakes to their exact capture locations. We recorded snout-vent length [SVL], tail length, mass, determined sex, and gave each snake a unique rattle color pattern, which allowed for visual identification in the event of repeated detections during the same season. We permanently marked all snakes by subcutaneously inserting Passive Integrated Transponder (PIT) tags (HPT8, Biomark, Boise, Idaho, USA).

We transported a subset of adult snakes to a veterinary clinic, where the veterinarian anesthetized them with isoflurane administered by an anesthesia machine and implanted them with VHF radio transmitters. Radios ranged in size from 3.5 to 4.5 g and were only implanted if they weighed less than 5% of the body mass of the snake (n = 23; models SOPI-2140 and 2190; Wildlife Materials International, Murphysboro, Maryland, USA; and n = 3; model IMP-CHP-6P; Telonics, Mesa, Arizona, USA). We implanted radio transmitters designed to operate from 244 to 355 d in 19 *C. pyrrhus* (12 males,



FIGURE 3. Example of the complexity of terrain in the Tinajas Altas Mountains, Yuma County, Arizona, USA. (Photographed by Austin B. Smith).

seven females). We implanted multiple radios in four snakes over the course of the study due to limited battery lifespan. After a 1-3-d recovery and post-surgery evaluation, we returned the snakes to their capture location.

Telemetry.—We conducted telemetry from October 2017 to May 2019, using Advanced Telemetry Systems (Isanti, Minnesota, USA) receivers and Telonics antennas (Flexible-H or Rigid-H). We focused our efforts from March through May during the C. pyrrhus mating season when they are most active (Klauber 1972; Goldberg 2000; Glaudas and Rodríguez-Robles 2011). We tracked snakes 4 d/ week from 19 March to 31 May 2018 and 25 March to 8 May 2019 (hereafter, spring). We tracked snakes intermittently during the remainder of the year (i.e., when snakes are less active) to keep track of their general location until the subsequent mating season. During the spring, we defined three daily survey periods: (1) morning (0600-1100); (2) afternoon (1100-1600); and (3) evening (1600-2100), and we tracked snakes during two haphazardly chosen survey periods each day, ensuring approximately equal observations per period. We took care to observe telemetered snakes as unobtrusively as possible to avoid affecting their behavior.

For each telemetered snake observation, we recorded date, time, location (UTMs, datum NAD83), air temperature (TA; shaded 1-m above ground), ground temperature (TG; shaded 1-cm above ground), and percentage cloud cover. We recorded one of three habitat types in which the snake was found: (1) wash, which also included steep canyon drainages with loose sand; (2) bajada, an area where alluvial fans line the mountain front (Phillips and Comus 2000); and (3) slope, an area with an incline generally covered in boulders and rocks. We also recorded cover type (boulder, burrow, crevice, packrat [Neotoma spp.] midden, vegetation, other, or none) and species of vegetation cover, if applicable. To assist in evaluating susceptibility to collection, we created an index to assess how visible the snake was upon each observation, referred to hereafter as visibility. The index was recorded on a scale from 0-10: none (0) = hidden; low (1-3) = visible in crevice or under dense cover; medium (4-6) = under light cover; high (7-9) = in open; very high (10) =moving or rattling. All observations were made by one of six observers familiar with the scale.

analysis.—We **Statistical** compiled and summarized data for all telemetered snakes from October 2017 through May 2019. We evaluated habitat data using all spring data combined. For activity area, core area, and movement calculations, we separated the active spring seasons (19 March to 31 May 2018 and 25 March to 8 May 2019) by year (hereafter spring 2018 and spring 2019). We completed all statistical analyses using SPSS (IBM Corp. Released 2016. IBM SPSS Statistics for Windows, Version 23.0.; Armonk, New York, USA) with $\alpha = 0.05$ and present all means with standard errors.

To evaluate habitat use and visibility, we combined all spring data and only used data for snakes with > 20 encounters for statistical analyses. We compared temperatures across survey periods (morning, afternoon, and evening) using Analysis of Variance (ANOVA) and used Dunn-Bonferroni Post-hoc analyses if a significant difference was found. We calculated the percentage weighted average (weighted per individual snake) for each parameter: habitat type, cover type, vegetation type, and visibility. We used individual snake weighted averages to account for individual variation and prevent skewing the data. We used Chi-squared tests to determine whether habitat type differed between years and whether cover type and snake visibility differed between survey periods. If a significant difference was found among groups, we used sequential Chi-square tests to determine which groups differed. For these analyses, we combined the use of burrow and packrat midden for cover type (0.3%) of observations) and the high and very high visibility indices (< 0.2% of observations) to meet sample size assumptions of the test.

We used two methods for home range estimates. Because of the limited spatial ecology literature on C. pyrrhus, we calculated 100% Minimum Convex Polygons (MCPs; Jenrich and Turner 1969; Reinert 1992) for each snake with > 20 observations (n = 13) across the entire study period (i.e., active and less-active seasons) to provide an overview of the estimated area used by individuals. Because MCPs assume the entire area is equally used, however, we also calculated Kernel Density Estimates (KDEs) to account for the probability snakes were disproportionately found in a given area (Powell 2000). We calculated 95% and 50% (activity and core areas, respectively) KDEs using the operating smoothing factor with the reference bandwidth (href; Kie et al. 2010; Kie 2013) for snakes with > 20

observations in spring 2018 (n = 9) and spring 2019 (n = 7). Home range estimates were calculated using the adehabitatHR package (v.0.4.19, Calenge 2006) in the R programming environment (R Development Core Team 2019).

To evaluate movement, we calculated the maximum distance moved between consecutive dates (i.e., total distance moved from the first encounter to the second encounter within 24 h), total distance traveled, and mean distance moved per day (i.e., total distance moved divided by the total number of days monitored; Reinert 1992). Because of unequal sample sizes, we compared male and female home ranges and movements per active spring season using Kruskal-Wallis tests. We compared spring 2018 and spring 2019 home ranges and movements using Two-sample *t*-tests assuming unequal variances. We derived data for movement patterns using ArcMap 10.7.1 with the Tracking Analyst extension (Esri, Redlands, California, USA). All means are given \pm standard error.

RESULTS

Telemetry.—From 1 October 2017 through 8 May 2019, we tracked 19 adult C. pyrrhus, resulting in 1,006 observations. We made 739 observations (n =13 snakes with > 20 observations) across the 2018 and 2019 spring seasons, including approximately 2,085 h of survey time. Observations were approximately evenly split among morning (n = 270), afternoon (n = 243), and evening (n = 226) survey periods. Conducting telemetry during different survey periods throughout the day allowed us to observe active snakes across various temperatures (TA = 13.6° - 37.8° C; TG = 15.3° – 42.8° C). Ground temperatures were significantly different between survey period (F2,734 = 200.6, P < 0.001). Morning survey period temperatures were significantly lower than afternoon temperatures (adjusted P < 0.001) and evening temperatures (adjusted P < 0.001) and afternoon survey period temperatures were significantly higher than evening temperatures (adjusted P < 0.001; mean morning TG = $25.9^{\circ} \pm 0.3^{\circ}$ C; mean afternoon TG = $33.9^{\circ} \pm 0.3^{\circ}$ C; mean evening TG = $29.2^{\circ} \pm 0.3^{\circ}$ C).

Habitat use and visibility.—Although *C. pyrrhus* used all three habitat types, we located snakes more frequently on slopes (65%) than in washes (23%) or bajadas (11%). We observed snakes across a range of elevations during the active spring seasons (mean = 418.1 ± 1.7 m; range of values 356.1-553.7 m).

Habitat use and elevation varied among individual snakes. All but three snakes used slopes for most of the active spring season; only two snakes used the wash (Snake 7: 49% and Snake 9: 60%), and one snake used the bajada (Snake 19: 65%) more often than the slope. We captured these three snakes at the lowest mean elevations (Snake $7 = 397.9 \pm 1.2$ m; Snake $9 = 393.9 \pm 3.8$ m; and Snake 19 = 368.6 \pm 3.8 m). Two snakes only used the slope habitat, and represented the highest mean elevations recorded (Snake $8 = 497.6 \pm 6.7$ m; Snake $12 = 494.0 \pm 3.1$ m). There was a strong association between habitat type and year ($\chi^2 = 65.85$, df = 2, P < 0.001). Snakes used slope habitat during the 2018 active spring season (75% of observations) more often than in 2019 (47%). In contrast, snakes used the wash and bajada habitats less in 2018 (wash = 19%, bajada = 5%) than in 2019 (wash = 36%, bajada = 17%).

Snakes were under cover in most of the encounters (90%), with little variation in cover type across individual snakes. Snakes frequently used boulders (57%) and vegetation (24%), but other cover included crevices (8%), burrows (1%), and packrat middens (<1%). For C. pyrrhus that used vegetation as cover, Elephant Tree (Bursera microphylla; 16%), Catclaw Acacia (Senegalia greggii; 14%), Creosote Bush (Larrea tridentata; 12%), Brittlebush (Encelia farinosa; 11%), and Desert Lavender (Hyptis emoryi; 8%) were the most frequently used (Table 1). We found a strong association between cover type and daily survey period ($\chi^2 = 27.84$, df = 8, P = 0.001). Sequential Chi-square tests revealed a significant difference in use of cover between morning and afternoon ($\chi^2 = 21.89$, df = 4, adjusted P < 0.001) and between afternoon and evening ($\chi^2 = 22.33$, df = 4, adjusted P < 0.001); however, there was not a significant difference in cover use between morning and evening ($\chi^2 = 3.94$, df = 4, adjusted P = 0.413). Snakes used cover significantly more in the afternoon (97%) as temperatures increased than in the morning (86%) or evening (86%). Visibility varied little across individual snakes. Most frequently, snakes could not be seen (30%) or had low (26%) or medium visibility (26%); snakes were highly visible only 18% of the time. There was a strong association between visibility and survey period ($\chi^2 = 20.08$, df = 6, P = 0.003). Sequential Chi-square tests revealed a significant difference in snake visibility between morning and afternoon ($\chi^2 = 14.40$, df = 3, adjusted P = 0.002) and between morning and evening ($\chi^2 =$ 15.63, df = 3, adjusted P = 0.001); however, there was not a significant difference in snake visibility

TABLE 1. Use of vegetation cover by Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) in the Tinajas Altas Mountains, Yuma County, Arizona, USA, during spring (March to May) 2018 and 2019. We calculated data from the 24% of total observations of snakes in vegetation, presented in order of largest to smallest.

Scientific name (common name)	Percentage use
Bursera microphylla (Elephant Tree)	16.4
Senegalia greggii (Catclaw Acacia)	14.3
Larrea tridentata (Creosote Bush)	11.7
Encelia farinosa (Brittlebush)	11.1
Hyptis albida (Desert Lavender)	8.4
Rhus kearneyi (Desert Sumac)	4.6
Olneya tesota (Ironwood)	4.4
Ambrosia dumosa (White Bursage)	4.0
Unknown	3.6
Parkinsonia florida (Blue Palo Verde)	3.4
Ephedra aspera (Mormon Tea)	2.7
Atriplex polycarpa (Desert Saltbush)	2.6
Sphaeralcea ambigua (Desert Globemallow)	2.6
Agave deserti (Desert Agave)	2.1
Tridens muticus (Slim Tridens)	1.5
Ambrosia ilicifolia (Holly-leaf Bursage)	1.0
Carnegia giantea (Saguaro)	1.0
Justicia californica (Chuparrosa)	1.0
<i>Cylindropuntia acanthocarpa</i> (Buckhorn Cholla)	0.8
Bebbia juncea (Sweetbush)	0.8
Fouquieria splendens (Ocotillo)	0.8
Prosopis glandulosa (Honey Mesquite)	0.4
Hesperocallis undulata (Desert Lily)	0.3
Ditaxis lanceolata (Narrowleaf Ditaxis)	0.2
Galium spp. (bedstraw)	0.2
Lycium macrodon (Desert Wolfberry)	0.2

between afternoon and evening ($\chi^2 = 2.07$, df = 3, adjusted P = 0.558). Snakes were significantly more visible in the morning (42%) and evening (40%) surveys than in the afternoon surveys (19%; Fig. 4).

Home range and movement patterns.—The 100% MCP estimates varied across individuals (nine males, four females; 927 total observations; Fig. 5). The 100% MCP for all snakes ranged from 0.91 to 13.74 ha (mean = 4.84 ± 1.20 ha; n = 13; Table 2). The 95% (activity areas) KDEs for spring 2018 and 2019 for females and males ranged from 1.4 to 57.3 ha and 0.1 to 20.1 ha, respectively (Tables 3 and 4). The 50%



FIGURE 4. Survey period and percentage visibility of Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) for all spring (March to May 2018 and 2019) observations in the Tinajas Altas Mountains, Yuma County, Arizona, USA.

(core areas) KDEs for both springs ranged from 0.3 to 13.1 ha for females and 0.03 to 4.4 ha for males (Tables 3 and 4). There was no significant difference between the size of male and female activity or core areas for spring 2018 (n = 9) or 2019 (n = 7; Tables 3 and 4). Additionally, the size of activity and core areas did not differ between spring 2018 and 2019 (Table 5).

Across the active spring seasons, the maximum distance moved ranged from 10 to 556 m, the total distance traveled ranged from 229 to 2351 m, and the mean distance moved per day ranged from 10 to 90 m. We found no significant differences in male

TABLE 2. Characteristics and Minimum Convex Polygon (MCP; 100%) home range estimates for 13 Southwestern Speckled Rattlesnake (*Crotalus pyrrhus*) from October 2017 to May 2019 in the Tinajas Altas Mountains, Yuma County, Arizona, USA. Abbreviations are SVL = snout-vent length, M = male, F = Female, and Obs = number of observations.

ID	Sex	SVL (mm)	Initial mass (g)	Obs	Days tracked	MCP (ha)
1	М	521	137	62	239	13.6
2	F	481	70	62	395	13.7
3	М	498	116	40	213	2.0
7	F	487	102	140	585	3.4
8	F	455	77	51	280	1.9
9	М			43	71	1.41
10	М	533	104	137	584	3.4
12	М	482	83	29	207	1.5
13	М	473	95	83	473	6.3
15	М	535	115	123	473	2.9
19	F	574	115	63	473	0.9
20	М	522	125	49	45	4.9
23	М	552	120	45	45	7.0



FIGURE 5. Home range estimates for each of 23 Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) using 100% Minimum Convex Polygons from October 2017 to May 2019 in the Tinajas Altas Mountains, Yuma County, Arizona, USA.

TABLE 3. Movement and home range parameters of nine Southwestern Speckled Rattlesnakes (Crotalus pyrrhus; > 20 observations for
each) from March 2018 to May 2018 in the Tinajas Altas Mountains, Yuma County, Arizona, USA. Home range estimates include 95%
(activity area) and 50% (core area) Kernel Density Estimates. Statistical comparisons between sexes are Kruskal-Wallis (K-W) tests (H
and P values) with all dfs = 1. Abbreviations are Obs = number of observations, DT = number of days tracked, MD = maximum distance
moved, TD = total distance moved, MD/d = mean distance moved per day, AA = activity area, CA = core area, F = female, M = male,
and $SE =$ standard error.

Snake ID	Obs	DT	MD (m)	TD (m)	MD/d (m)	AA (ha)	CA (ha)
Females							
2	45	26	556	2351	90.4	57.3	13.1
7	55	33	118	857	26.0	3.7	1.0
8	40	29	47	515	17.8	5.3	1.4
Mean	47	29	240	1241	44.7	22.1	5.16
SE	4	2	159	564	23.0	17.6	4.0
Males							
1	53	32	131	1187	37.1	12.7	2.8
3	30	20	19	528	26.4	7.9	2.0
9	43	24	129	928	38.7	2.8	0.5
10	50	33	115	811	24.6	1.1	0.2
12	21	17	21	290	17.1	2.2	0.6
15	48	31	96	730	23.5	4.5	1.3
Mean	41	26	85	746	27.9	5.2	1.2
SE	5	3	21	128	3.4	1.8	0.4
Both Sexes							
Mean	43	27	137	911	33.5	10.8	2.5
SE	4	2	55	200	7.5	5.9	1.4
K-W Test	-	-	0.600 (0.439)	0.267 (0.606)	0.067 (0.796)	1.067 (0.302)	1.067 (0.302)

TABLE 4. Movement and home range parameters of nine Southwestern Speckled Rattlesnakes (Crotalus pyrrhus; > 20 observations
for each) from March 2019 to May 2019 in the Tinajas Altas Mountains, Yuma County, Arizona, USA. Home range estimates include
95% (activity area) and 50% (core area) Kernel Density Estimates. Statistical comparisons between sexes are Chi-square tests (χ^2 and
P values) with all dfs = 1. Abbreviations are Obs = number of observations, DT = number of days tracked, MD = maximum distance
moved, TD = total distance moved, MD/d = mean distance moved per day, AA = activity area, CA = core area, F = female, M = male,
and $SE = standard error.$

Snake ID	Obs	DT	MD (m)	TD (m)	MD/d (m)	AA (ha)	CA (ha)
Females							
7	51	22	70	764	34.7	1.9	0.4
19	49	22	37	380	17.3	1.4	0.3
Mean	50	22	54	572	26.0	1.6	0.3
SE	1.0	0	17	192	8.7	0.2	0.1
Males							
10	50	22	10	229	10.4	0.1	0.03
13	52	22	139	1650	75.0	7.1	1.5
15	51	22	29	396	18.0	1.2	0.3
20	49	22	134	1956	88.9	10.4	2.4
23	45	22	217	1581	71.9	20.1	4.4
Mean	49	22	106	1162	52.8	7.8	1.7
SE	1.0	0	38	354	16.1	3.6	0.8
Both Sexes							
Mean	50	22	91	994	45.2	6.0	1.3
SE	1.0	0	28	271	12.3	2.7	0.6
Chi-Square	-	-	0.150 (0.699)	0.600 (0.439)	0.600 (0.439)	0.150 (0.699)	0.150 (0.699)

and female maximum distance moved, total distance traveled, or mean distance moved per day (Tables 3 and 4). We found no significant differences in maximum distance traveled, mean daily movement, or total distance traveled between years (Table 5). In 2018, however, one female (Snake 2) moved far greater distances than the others (Table 3).

DISCUSSION

Although they may be locally abundant, several snake species in Arizona are considered vulnerable in the Arizona State Wildlife Action Plan, partly due to a lack of current population data (Jones and Goode 2020; Arizona Game and Fish Department 2022). Knowledge of habitat use and home range size requirements is critical for making informed ecological management decisions (Weatherhead and Prior 1992; Durbian et al. 2008; Lee et al. 2011), but effective management and protection pose challenges when basic, yet difficult-to-determine information about a species is unavailable (e.g., survivorship, habitat requirements, etc.). In addition, most snake species are inherently challenging to study because they are cryptic and often difficult to detect and

capture (Parker and Plummer 1987; Steen 2010).

Before this study, little was known about the ecology of *C. pyrrhus* in southwestern Arizona (Cochran 2019). Our study revealed habitat features (e.g., slope habitat, boulders, *Bursera microphylla*, and *Senegalia greggii*) that are most often used by *C. pyrrhus* in the TAs, and how much area may be required for an individual home range of a snake. The 13 telemetered snakes (nine males, four females) we tracked covered a total area of 49 ha (based on MCP home ranges). Collectively, our work advances our understanding of habitat use and home range estimates and informs the vulnerability of *C. pyrrhus* to collecting pressure.

Habitat and resource use.—Our study revealed similarities and differences in the ecology of *C*. *pyrrhus* in the TAs compared to other parts of their range. Snake visibility and cover use varied as temperatures fluctuated throughout the day, consistent with what has been observed in other rattlesnake studies (e.g., Moore 1978; Beck 1995). As expected for this largely saxicolous snake, they used slope habitat, including boulders and shrubs, as cover for shade and hunting, similar to *C. pyrrhus* elsewhere

	Activity area (ha)	Core area (ha)	Maximum distance (m)	Total distance (m)	Mean distance moved/day (m)
Spring 2018					
Mean	10.85	2.54	137	911	45.2
SE	5.93	1.35	54	200	12.3
Spring 2019					
Mean	6.02	1.32	91	994	33.5
SE	2.74	0.60	28	271	7.5
t-statistic (df)	0.739 (11)	0.829 (11)	0.749 (12)	-0.246 (12)	-0.089 (10)
P-value	0.475	0.425	0.468	0.809	0.437

TABLE 5. Movement and home range parameters for Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) in the Tinajas Altas Mountains, Yuma County, Arizona, USA, from March 2018 to May 2018 (Spring 2018) and March 2019 to May 2019 (Spring 2019). Mean home range estimates include (95%) activity area and (50%) core area kernel density estimations. Mean movements for spring 2018 and 2019 include maximum distance (m), defined as the maximum distance traveled in a 24-h, total distance traveled (m), and mean distance moved per day (m). Comparison of variables between years from Two-sample t-tests assuming unequal variances.

(McCrystal and McCoid 1986; Meik and Babb 2020). When snakes used vegetation as cover, 30% of the observations included snakes at the base of Bursera microphylla, or at the base or within Senegalia greggii. Although the diet of C. pyrrhus across their range consists primarily of mammals in addition to lizards and insects (Klauber 1936; 1972; DeVault and Krochmal 2002), in the TAs, their diet includes a significantly higher proportion of birds (Cochran 2019). On three occasions, snakes were found coiled in ambush posture at about 1.5-2 m high in S. greggii, presumably in ambush mode for birds. In 2019, we observed one C. pyrrhus attempting to prey on a Black-chinned Sparrow (Spizella atrogularis), which ultimately was too large for the snake to ingest and was subsequently regurgitated.

Home range and movement patterns.—The effects of sex on the spatial ecology of rattlesnakes differ across and within species and populations. Most rattlesnake studies, including other *C. pyrrhus* studies, have found that males traveled farther and had larger home ranges than females during the mating season (e.g., Goode et al. 2008; Glaudas and Rodríguez-Robles 2011; Putman et al. 2013). We found no significant difference in activity area, core area, or movements between sexes, however, during either of the spring mating seasons of our study. This lack of sex-related differences in home range may be an artifact of small sample size, or because males did not have to travel far to locate prospective mates.

We found no significant differences in movement patterns between sexes during either spring mating season, similar to home range estimates. Comparatively, movement patterns of *C. pyrrhus* varied between sexes in the Mojave Desert (Glaudas and Rodríguez-Robles 2011). Mean daily distances traveled by both sexes during the mating season in our study and in the Mojave Desert (Glaudas and Rodríguez-Robles 2011) were similar (38 m and 26 m, respectively). Mean daily distances moved by females and males in the TAs, however, were greater than those in the Mojave Desert (females 35 m versus 17 m; males 40 m versus 30 m, respectively).

The effects of precipitation on rattlesnake movements are poorly understood, but where it has been studied, effects appear strong but contradictory across different habitats. For instance, in Tiger Rattlesnakes (C. tigris), typically found in desert rocky slopes and canyons in Arizona, males moved more in a wet year than a dry year (Goode et al. 2008), while in a montane ecosystem, Twin-spotted Rattlesnakes (C. pricei) males moved farther during a dry year (Prival et al. 2002). Our study experienced one slightly below average and one unusually wet winter season. Average winter precipitation (December, January, and February; measured at Tacna 3 NE, Arizona (station number 028396), approximately 72 km east of Yuma, Arizona) is approximately 1.1 cm (https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?az8396). The 2017-2018 winter season precipitation was slightly below average (0.9 cm), whereas the winter of 2018–2019 was unusually wet (2.7 cm). Despite differences in precipitation, movement patterns did not differ significantly between years. We tracked three snakes (one female and two males) across both of our slightly dry and wet active spring seasons. Each of these snakes had more extensive activity and core areas in the spring of 2018 than in 2019 (Fig. 6), likely because there was reduced prey availability during the drier year, causing snakes to travel longer distances in search of food (e.g., Prival et al. 2002;



FIGURE 6. Comparison of home range estimates for one female (Snake 7) and two male (Snake 10 and 15) Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) using 95% (activity area) and 50% (core area) Kernel Density Estimates for the (A) 2018 (near average winter precipitation) and (B) 2019 (above average winter precipitation) spring seasons (March to May) in the Tinajas Altas Mountains, Yuma County, Arizona, USA.

Sperry and Weatherhead 2008).

Our study is one of only a few to study C. pyrrhus. Greenberg and McClintock (2008) investigated C. pyrrhus in the Coachella Valley, California, USA (Lower Colorado River Valley subdivision of the Sonoran Desert), and Glaudas and Rodríguez-Robles (2011) worked in the Eldorado Mountains in the eastern Mojave Desert, Nevada, USA. Compared to annual MCP home range estimates in the Coachella Valley (0.9-81 ha; mean = 20 ha; Greenberg andMcClintock 2008), MCP home range estimates in our study were considerably smaller (0.9-13.7 ha; mean = 4.8 ha). Male activity areas for our study were similar in size to C. pyrrhus in the Mojave Desert population during the mating season (6.5 ha vs. 9.7 ha \pm 9.4), yet considerably larger for females (11.9 ha vs. 3.0 ha \pm 7.1; Glaudas and Rodríguez-Robles 2011), but this is likely an artifact of female Snake 2 that moved much greater distances than all other snakes. We conducted post-hoc significance tests that did not yield different results when Snake 2 was removed from our movement analyses; however, if we remove Snake 2, the average female activity area (3.1 ha) would be almost identical to Mojave Desert females (Glaudas and Rodríguez-Robles 2011). Nonetheless, home range estimates for C. pyrrhus are limited to three studies, including this one, so it would be overly optimistic to draw firm comparisons. Future research estimating the home ranges of C. pyrrhus populations throughout their geographic distribution would contribute to our understanding of the spatial ecology of C. pyrrhus.

Conservation and management.-The primary mission of BMGR is aviation training with limited on-the-ground disturbance, and public access is tightly controlled (Ripley 2015; CEMML 2018). Consequently, these snakes (and other natural resources) are largely protected from many factors that put other snake populations at risk, such as excessive recreational pressure or development. Nonetheless, the attractive appearance of C. pvrrhus in the TAs has created the threat of collection for individual use and the hobby or commercial trade. Jones and Goode (2020) describe the considerable interest in collecting and the commercial exploitation of snakes in Arizona, in addition to the lack of data to determine the effects of collection on wild populations. Wildlife trafficking is a growing and prominent threat to species worldwide (Muth and Bowe 1998; Wyatt and Cao 2015). This population may be especially vulnerable to collection because of its restricted distribution, magnified by C. pyrrhus life-history characteristics, including low fecundity and prolonged time to reach the age of reproduction (Goldberg 2000; Meik and Babb 2020).

Our study site is in a portion of the TAs more frequently visited by individuals seeking *C. pyrrhus* (Michael Sumner, pers. comm.); however, we found that snake visibility was medium (26%), low (26%), or none (30%) for the majority of observations, and snakes only rattled on four of 1,006 observations. Additionally, the remote and rugged nature of the TAs makes it challenging to access most of the mountain range (Felger et al. 2012), likely restricting most collecting to easily accessible sites. Future demographic studies will be required to determine how many snakes are necessary to maintain a stable population and how the collection of these snakes affects their population viability. Our data suggest that the secretive nature and relatively inaccessible microhabitats of these snakes, along with the limited public access onto the BMGR, may provide a mechanism to limit local population-level losses and thus maintain healthy *C. pyrrhus* populations.

Acknowledgments.-Ashley A. Grimsley-Padron and Austin B. Smith contributed equally to the analysis and writing of this manuscript. The Heritage Fund and the State Wildlife Grant programs of the Arizona Game and Fish Department provided funding for this study. We are grateful to the many individuals who assisted with fieldwork, especially Alec Goodman, Morgan Sweet, Trent Adamson, and Sky Arnett-Romero. We thank Jeremy Pennell and Robert Law for logistical assistance and access to the study site and Cheryl Haugo, James Jarchow, and Heather Bjornebo for conducting surgeries at the Desert Veterinary Clinic in Yuma, Arizona, and Arizona Exotic Animal Hospital in Phoenix, Arizona. We thank Daniel Leavitt, Ryan O'Donnell, Pam Kennedy, Lisa Hodge, Keith Knutson, and Renee Wilcox for administrative assistance, Daniel Leavitt for assistance in study design, Sue Boe, Matt King, Joseph Holbrook, Mitchell Brunet, Patrick Fekety, and Sarah Baker for analytical guidance and expertise, and Sarah Baker, Daniel Leavitt, Ryan O'Donnell, and Jeremy Pennell for helpful comments on manuscript drafts.

LITERATURE CITED

- Arizona Game and Fish Department. 2022. Arizona Wildlife Conservation Strategy: 2022–2032. Arizona Game and Fish Department, Phoenix, Arizona, USA. 393 p.
- Beck, D.D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. Journal of Herpetology 29:211–223.
- Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.
- Center for Environmental Management of Military Lands (CEMML). 2018. U.S. Air Force Integrated Natural Resource Management Plan 2018–2023 Update: Barry M. Goldwater Range, Arizona. Colorado State University, Fort Collins, Colorado, USA. 280 p.

- Cochran, C. 2019. Variation in morphology, diet, and venom composition in *Crotalus pyrrhus* (Cope 1867). Ph.D. Dissertation, Loma Linda University, Loma Linda, California, USA. 159 p.
- DeVault, T.L., and A.R. Krochmal. 2002. Scavenging by snakes: an examination of the literature. Herpetologica 58:429–436.
- Durbian, F.E., R.S. King, T. Crabill, H. Lambert-Doherty, and R.A. Seigel. 2008. Massasauga home range patterns in the Midwest. Journal of Wildlife Management 72:754–759.
- Felger, R.S., T.R. Van Devender, B. Broyles, and J. Malusa. 2012. Flora of Tinajas Altas, Arizona a century of botanical forays and forty thousand years of *Neotoma* chronicles. Journal of the Botanical Research Institute of Texas 6:157–257.
- Glaudas, X., and J.A. Rodríguez-Robles. 2011. Vagabond males and sedentary females: spatial ecology and mating system of the Speckled Rattlesnake (*Crotalus mitchellii*). Biological Journal of the Linnean Society 103:681–695.
- Goldberg, S.R. 2000. Reproduction in the Speckled Rattlesnake, *Crotalus mitchellii* (Serpentes: Viperidae). Bulletin of the Southern California Academy of Sciences 99:101–104.
- Goode, M., J.J. Smith, and M. Amarello. 2008. Seasonal and annual variation in home range and movements of Tiger Rattlesnakes (*Crotalus tigris*) in the Sonoran Desert of Arizona. Pp. 327–334 In The Biology of Rattlesnakes. Hayes, W.K., K.R. Beaman, M.D. Cardwell, and S.P. Bush (Eds.). Loma Linda University Press, Loma Linda, California, USA.
- Greenberg, D.B., and W.J. McClintock. 2008. Remember the third dimension: terrain modeling improves estimates of snake home range size. Copeia 2008:801–806.
- Hierink, F., I. Bolon, A.M. Durso, R. Ruiz de Castañeda, C. Zambrana-Torrelio, E.A. Eskew, and N. Ray. 2020. Forty-four years of global trade in CITES-listed snakes: trends and implications for conservation and public health. Biological Conservation 248:108601. https://doi. org/10.1016/j.biocon.2020.108601.
- Jenrich, R.I., and F.B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227–237.
- Jones, T.R., and M. Goode. 2020. Conservation. Pp. 33–51 In Snakes of Arizona. Holycross, A.T., and J.C. Mitchell (Eds.). ECO Publishing, Rodeo, New Mexico, USA.

- Kie, J.G., J. Matthiopoulos, J. Fieberg, R.A. Powell, F. Cagnacci, M.S. Mitchell, J-M. Gaillard, and P.R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of The Royal Society 365:2221–2231.
- Kie, J.G. 2013. A rule-based *ad hoc* method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:13. https://doi. org/10.1186/2050-3385-1-13.
- Klauber, L.M. 1936. *Crotalus mitchellii*, the Speckled Rattlesnake. Transactions of the San Diego Society of Natural History 8:149–184.
- Klauber, L.M. 1972. Rattlesnakes: Their Habits, Life Histories and Influence on Mankind. 2nd Edition. Volume 1. University of California Press, Berkeley, California, USA.
- Lee, H-J., J-H. Lee, and D. Park. 2011. Habitat use and movement patterns of the viviparous aquatic snake, *Oocatochus rufodorsatus*, from northeast Asia. Zoological Science 28:593–599.
- Marshall, B.M., C. Strine, and A.C. Hughes. 2020. Thousands of reptile species threatened by underregulated global trade. Nature Communications 11:4738. https://doi.org/10.1038/s41467-020-185-23-4.
- McCrystal, H.K., and M.J. McCoid. 1986. *Crotalus mitchellii*. Catalogue of American Amphibians and Reptiles 388:1–4.
- Meik, J.M. 2016. Southwestern Speckled Rattlesnake (*Crotalus pyrrhus*). Species account. Pp. 531–562 In Rattlesnakes of Arizona. Volume 1. Schuett, G.W., M.J. Feldner, C.F. Smith, and R.S. Reiserer (Eds.). ECO Publishing, Rodeo, New Mexico, USA.
- Meik, J.M., and R.D. Babb. 2020. Crotalus pyrrhus (Southwestern Speckled Rattlesnake). Species account. Pp. 588–599 In Snakes of Arizona. Holycross, A.T., and J.C. Mitchell (Eds.). ECO Publishing, Rodeo, New Mexico, USA.
- Moore, R.G. 1978. Seasonal and daily activity patterns and thermoregulation in the Southwestern Speckled Rattlesnake (*Crotalus mitchellii pyrrhus*) and the Colorado Desert Sidewinder (*Crotalus cerastes laterorepens*). Copeia 1978:439–442.
- Muth, R.M., and J.F. Bowe, Jr. 1998. Illegal harvest of renewable resources in North America: towards a typology of the motivations for poaching. Society and Natural Resources 11:9–24.
- Parker, W.S., and M.V. Plummer. 1987. Population ecology. Pp. 253–301 In Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins,

and S.S. Novak (Eds.). The Blackburn Press, Caldwell, New Jersey, USA.

- Petersen, C.E., S.M. Goetz, M.J. Dreslik, J.D. Kleopfer, and A.H. Savitzky. 2019. Sex, mass, and monitoring effort: keys to understanding spatial ecology of Timber Rattlesnakes (*Crotalus horridus*). Herpetologica 75:162–174.
- Phillips, S.J., and P.W. Comus. 2000. A Natural History of the Sonoran Desert. Arizona-Sonora Desert Museum Press, Tucson, Arizona, USA.
- Powell, R.A. 2000. Animal home ranges and territories and home range estimators. Pp. 65– 110 In Research Techniques in Animal Ecology: Controversies and Consequences. Boitani, L., and T. Fuller (Eds.). Columbia University Press, New York, New York, USA.
- Prival, D.B., M.J. Goode, D.E. Swann, C.R. Schwalbe, and M.J. Schroff. 2002. Natural history of a northern population of Twinspotted Rattlesnakes, *Crotalus pricei*. Journal of Herpetology 36:598–607.
- Putman, B.J., C. Lind, and E.N. Taylor. 2013. Does size matter? Factors influencing the spatial ecology of Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*) in Central California. Copeia 2013:485–492.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation Statistical Computing, Vienna, Austria. https://www.R-project.org.
- Reinert, H. K. 1992. Radiotelemetric field studies of pitvipers: data acquisition and analysis. Pp. 185– 197 In Biology of the Pitvipers. Campbell, J.A., and E.D. Brodie, Jr. (Eds.). Selva, Tyler, Texas, USA.
- Ripley, J.D. 2015. Revealing military secrets: the little known history of the U.S. military in discovering, describing, and conserving native plants in Arizona. The Plant Press 38:1–5.
- Rizzolo, J.B. 2021. Effects of legalization and wildlife farming on conservation. Global Ecology and Conservation 25:e01390. https://doi.org/10.1016/j.gecco.2020.e01390.
- Sperry, J.H., and P.J. Weatherhead. 2008. Preymediated effects of drought on condition and survival of a terrestrial snake. Ecology 89:2770– 2776.
- Steen, D.A. 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herpetological Conservation and Biology 5:183–188.

Turner, R.M., and D.E. Brown. 1982. Tropicalsubtropical desertlands. Pp. 180–222 In Biotic Communities of the American Southwest - United States and Mexico. 1982. Desert Plants 4(1–4):1– 342. Special Issue. University of Arizona. Tucson, USA.

Weatherhead, P.J., and K.A. Prior. 1992. Preliminary observations of habitat use and movements of the

Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*). Journal of Herpetology 26:447–452.

Wyatt, T., and A.N. Cao. 2015. Corruption and Wildlife Trafficking. U4 Anti-Corruption ResourceCentre, Chr. Michelsen Institute, Bergen, Norway.



ASHLEY GRIMSLEY-PADRON is the Captive Wildlife Program Coordinator at the Arkansas Game and Fish Commission, Springdale, Arkansas, USA. She received her B.S. and M.S. in Biological Sciences from the University of Arkansas, Fayetteville, Arkansas, USA, where she studied Eastern Collared Lizards (*Crotaphytus collaris*). Ashley worked for 7 years at the Arizona Game and Fish Department, Phoenix, Arizona, USA, focusing much of her research on the ecology and management of desert reptiles. She continues her dedication to conservation and management of native wildlife and habitat through her current position. (Photographed by Ashley A. Grimsley-Padron).



AUSTIN SMITH received a B.S. in Geography with a concentration in Environmental Studies and a M.A.S. in Geographic Information Systems from Arizona State University, Tempe, Arizona, USA, and a M.S. in Zoology from the University of Wyoming, Laramie, Wyoming, USA. He is a research scientist in the Haub School of Environment and Natural Resources at the University of Wyoming. His work primarily focuses on the behavior and population and community ecology of mammalian carnivores across the Intermountain West of the USA. (Photographed by Kimberly L. Denningmann).



LIN PIEST received his Bachelor's Degree from the University of Missouri, Columbia, Missouri, USA, and his Master's Degree from the University of Arizona, Tucson, Arizona, USA, both in Wildlife Management. He had a 35-y career with the Arizona Game and Fish Department, Yuma, Arizona, USA, primarily as a nongame biologist working on a variety of monitoring and research projects with birds, bats, herps, and rodents. A major focus included conservation actions and monitoring for the Flat-tailed Horned Lizard (*Phrynosoma mcallii*). Lin is retired now and lives in herpetologist heaven near Tucson, Arizona. (Photographed by Kyla Garten).



MICHAEL INGRALDI received his B.S. and M.S. from the SUNY College of Environmental Science and Forestry, Syracuse, New York, USA, in Wildlife Management, and his Ph.D. in Forest Wildlife Management from Northern Arizona University, Flagstaff, Arizona, USA. Michael has worked 32 y for the Arizona Game and Fish Department, Phoenix, Arizona, USA, and is currently a Research Supervisor with the Wildlife Contracts Branch, where he has brought in over \$50 million in outside funding throughout his career. His primary responsibility is to design and implement fish and wildlife-related surveys, monitoring, research studies, and habitat restoration projects. (Photographed by Nora Clark).



TOM JONES received his B.S. and M.S. from Auburn University, Auburn, Alabama, USA, and Ph.D. from Arizona State University, Tempe, Arizona, USA. He is the Amphibians and Reptiles Program Manager for the Arizona Game and Fish Department, Phoenix, Arizona, USA, where for the last 19 y, he has overseen conservation and management of amphibians and reptiles in Arizona. (Photographed by Randall D. Babb).