In 2009, during the participation of a scientific congress in Chetumal (Quintana Roo, Mexico), Gunther Köhler went for a night cruise by car with Pablo M. Beutelspacher-García and was surprised by the many road-killed snakes they encountered. This prompted the authors to start a long-term project with nocturnal snake surveys at 15-day intervals along a 39 km road transect. Since they started the project in early 2010, the authors have encountered a total of 578 snakes (433 road-killed, 145 alive) along the study transect, representing 31 species. Pictured here is a road-killed individual of *Drymarchon melanurus*. © Gunther Köhler

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The Chetumal Snake Census: generating biological data from road-killed snakes. Part 1. Introduction and identification key to the snakes of southern Quintana Roo, Mexico

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ABSTRACT: On 13 February 2010, we started conducting ongoing nocturnal snake surveys at 15-day intervals along a 39 km road transect near the city of Chetumal, Quintana Roo, Mexico. During this time, we have encountered a total of 578 snakes (433 road-killed, 145 alive) representing 31 species (Boidae: 1 species; Colubridae: 13 species; Dipsadidae: 13 species; Elapidae: 1 species; Natricidae: 1 species; Viperidae: 2 species). All of the dead snakes found on the road were collected and preserved (except when the carcasses were decomposed or badly damaged). Subsequently, we dissected the collected specimens to examine their gonads and intestinal contents. In Part 1 of this series, we describe the methods and the study site, and define the objectives of the study. We present an overview of the snakes recorded between February of 2010 and June of 2016, and provide an identification key to the snake species known from or expected to occur in the Chetumal region. In the forthcoming parts of this series, we will present data on the external morphology, seasonality, spatial distribution, reproduction, and diet for each of the species collected during these surveys.

Key Words: Colubridae, diet, Dipsadidae, Elapidae, identification key, Mexico, monitoring, Natricidae, population dynamics, Quintana Roo, reproduction, snake survey, Viperidae

RESUMEN: A partir del 13 de febrero de 2010 hemos realizado muestreos nocturnos a intervalos de 15 días, para registrar serpientes a lo largo de un transecto de carretera de 39 km ubicado cerca de la ciudad de Chetumal, Quintana Roo, México. Como resultado, hemos encontrado un total de 578 serpientes (433 atropelladas, 145 vivas) de 31 especies (Boidae: 1 especie; Colubridae: 13 especies; Dipsadidae: 13 especies; Elapidae: 1 especie; Natricidae: 1 especie; Viperidae: 2 especies). Todos los ejemplares encontrados muertos sobre la carretera fueron colectado y preservados (excepto cuando los cadáveres estaban en avanzado estado de descomposición o muy destrozados). Posteriormente, realizamos disecciones a los ejemplares colectados, para examinar sus gónadas y el contenido estomacal. En la Parte 1 de esta serie, definimos los objetivos del estudio y describimos el sitio de muestreo y los métodos utilizados. Asimismo, presentamos un resumen de las serpientes registradas entre febrero de 2010 y junio de 2016, y proporcionamos claves de identificación para las especies de serpientes con distribución conocida o potencial en el área de estudio. En las próximas partes de esta serie, presentaremos datos sobre la morfología externa, estacionalidad, distribución espacial, reproducción y dieta de cada una de las especies registradas durante los muestreos.

Palabras Claves: Claves de identificación, Colubridae, dieta, dinámica poblacional, Dipsadidae, Elapidae, Mexico, muestreo y monitoreo de serpientes, Natricidae, Quintana Roo, reproducción, Viperidae

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INTRODUCTION

Roads lead to various adverse effects on fauna and flora, and the destruction of the environment by constructing a road is not the only threatening factor. Numerous edge effects can pose problems for the resident fauna and flora, as roads affect the microclimate, especially the temperature and humidity, and also generate light, noise, and chemical pollution. Moreover, the access of people to otherwise less accessible habitats results in additional disturbance and pollution (Mader, 1984), and the fragmentation of habitats caused by roads separates the populations into smaller subpopulations, resulting in reduced gene flow (Andrews, 1990; Epps et al., 2005). Road traffic causes fatalities among the resident animal species, and probably is the best-known and visible impact of roads upon wildlife. Forman and Alexander (1998) estimated that approximately one million vertebrates are killed on roads each day in the United States. The herpetofauna represents a substantial portion of the animals found dead on roads, and the type of habitat, as well as the taxonomic diversity and population density, influences the number of road-kills (Ashley and Robinson, 1996; Attademo et al., 2011; Colino-Rabanal and Lizana, 2012; Fahrig et al., 1995; Grosselet et al., 2008). Consequently, snake road mortality has garnered significant research attention (reviewed in Andrews et al., 2008).

Aside from generating information on the impact of roads based on casualties among snakes, however, studying the actual traffic victims can yield a wealth of biological data for the individual species. Surveys of snake carcasses on roads can provide an insight into community composition, species abundances, migratory and reproductive timing, clutch and litter sizes, diet, and population genetics (Bernardino and Dalrymple, 1992; Enge and Wood, 2002; Köhler, 2016).

Here we report data generated from road-killed snakes collected during a long-term study in southern Quintana Roo, Mexico.

MATERIALS AND METHODS

The study area is located northeast of the city of Chetumal, in the southeastern portion of the Yucatan Peninsula, Mexico (Fig. 1). The survey route includes a total of 39 km of paved road (mean road width = 7 m), with the coastal areas of the Caribbean Sea to the east and the lagoons near the town of Bacalar to the west. The road transect is divided into five sections. The first section is from Calderitas, a suburb of Chetumal, and along the coast in a northeasterly direction. The second section is from this coastal region up to Luis Echeverría, a small settlement northeast of Chetumal. The third section extends from southeast of Luis Echeverria to an intersection connecting this road with one that leads to Ursulo Galván, which represents the fourth section. Ursulo Galván is a settlement on the eastern banks of Laguna Guerrero. The fifth section is from the aforementioned intersection back to Calderitas. To gain a basic understanding of the traffic intensity among the five sections of the transect, we conducted a 24 h count

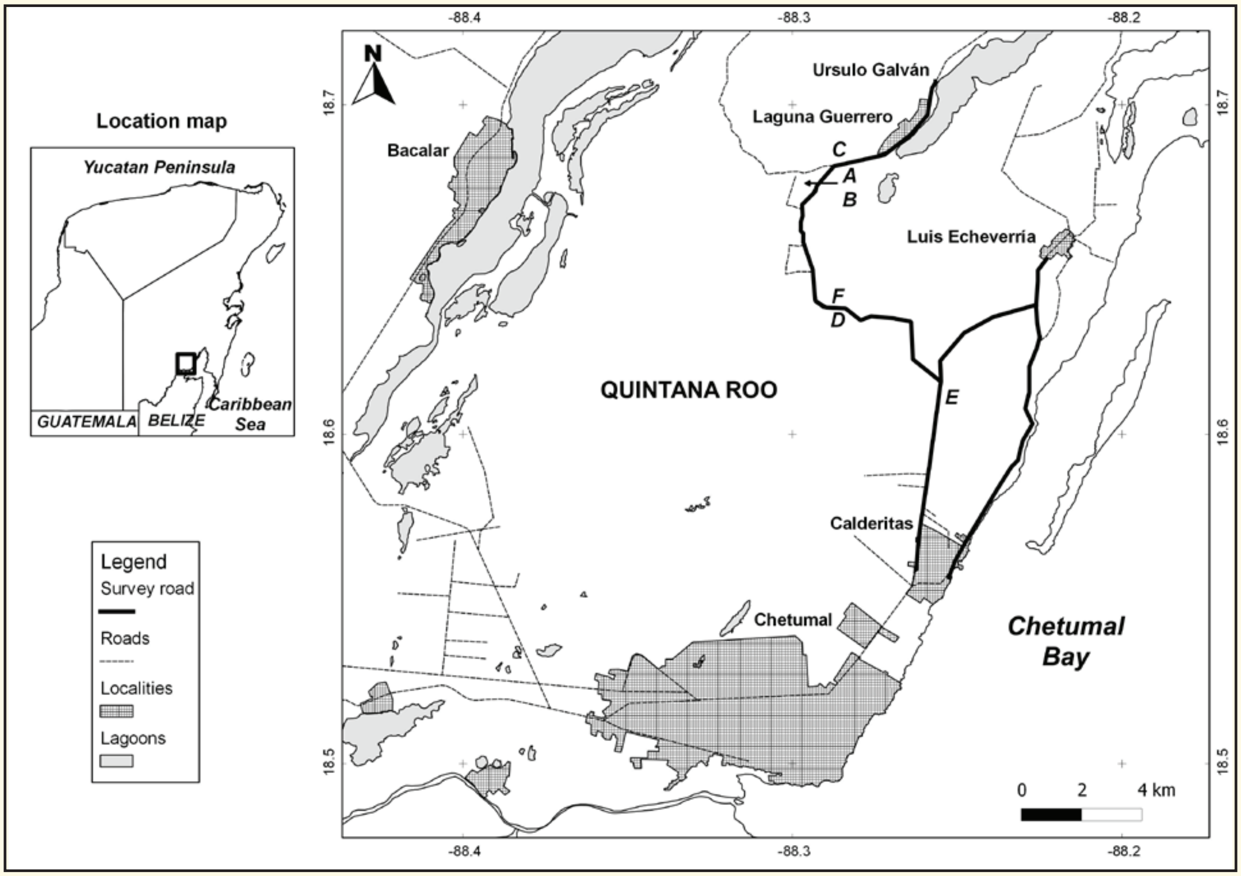

Fig. 1. Study site indicating the road transect in southern Quintana Roo, Mexico. Capital letters correspond to those in Fig. 3.

of the vehicles and motorbikes traversing each of these sections on three consecutive days (16–18 June 2015). We based our final designation for the vehicle intensity category for each of the portions, however, on observations conducted during road surveys from 2009 to 2016, even though the one-day traffic census was not congruent with these designations for all the portions of the transect (Table 1). We distinguished four categories of traffic intensity: (1) low traffic intensity, (2) moderate traffic intensity, (3) high traffic intensity, and (4) very high traffic intensity. We color-coded these four categories in Fig. 2.

Table 1. Traffic intensity categories of portions of studied road transect. Designation of vehicle intensity category for each portion was based on observations during road surveys from 2009 to 2016. The actual counts of vehicles and motorbikes were performed for 24 hours/portion on consecutive days (16–18 June 2015). See text for details.

Transect Portion	Intensity Category	Vehicles	Motorbikes	Total
1	Moderate	365	44	409
2	Low	15	4	19
3	High	226	136	362
4	Very high	399	178	577
5	Moderate	389	164	553

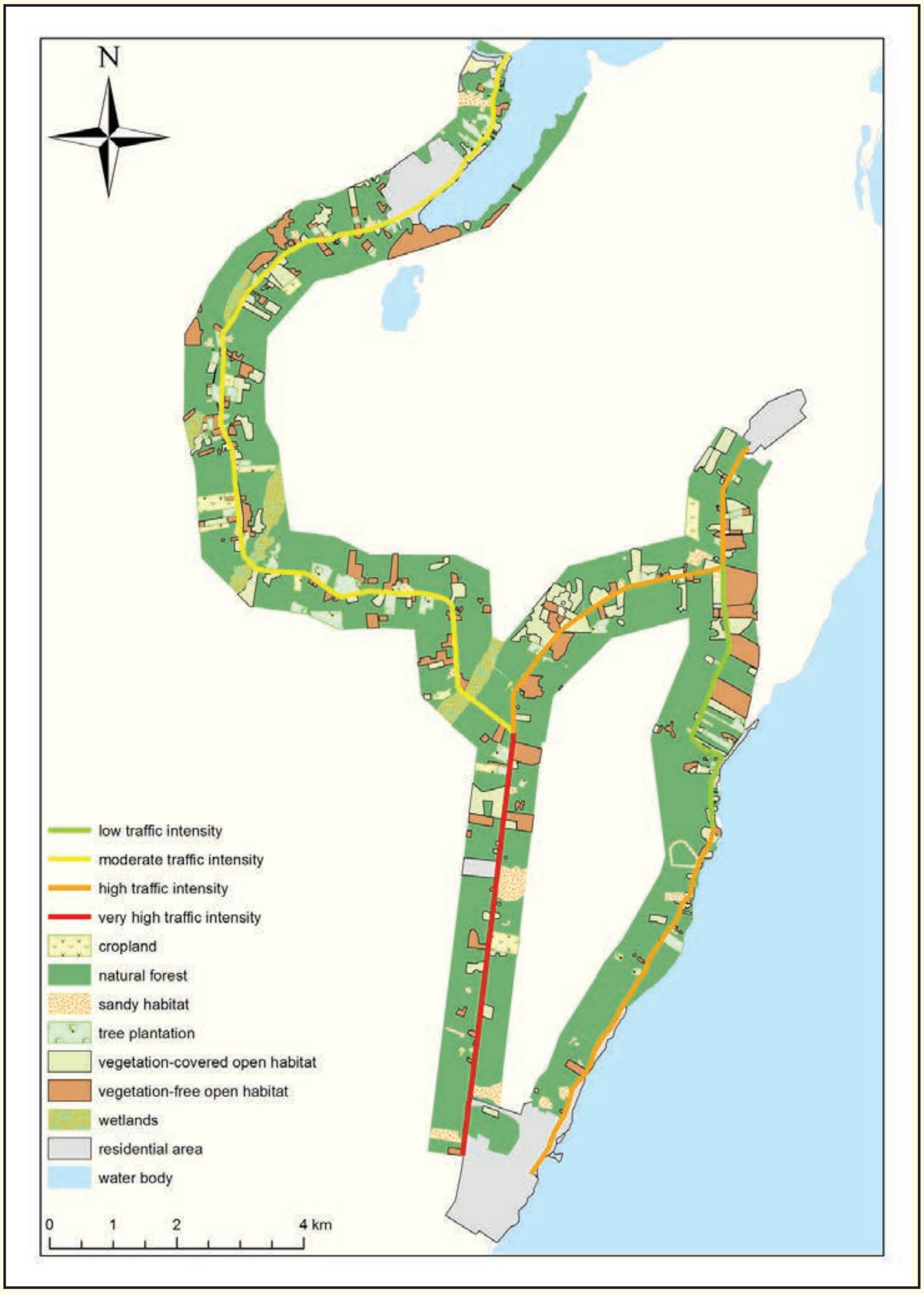

Fig. 2. Distribution of various habitats and differences in traffic intensity along the road transect.

The road transect passes through a mosaic of anthropogenically intervened environments, which are composed of secondary vegetation in different successional stages, some patches of slash and burn agriculture, a few forest plantations (e.g., *Cedrela odorata*, *Cocos nucifera*, *Cordia dodecandra* and *Swietenia macrophylla*,), small cattle ranches, wetlands, and villages (Fig. 3). For the spatial analyses, we distinguished eight different types of habitats along our road transect (proportion of whole area in parentheses): cropland (1.8%), residential areas (8.6%), wetlands (2.4%), tree plantations (3.6%), open, sandy habitat (2.1%), vegetation-covered open habitat (8.6%), vegetation-free open habitat (8.7%), and forest areas with closed canopy (64.2%). We recorded the ambient temperature and rainfall at the study site with the help of data loggers (Hobo) and rain gauges, respectively. We programmed the Hobo data loggers to record the ambient temperature at 20 min intervals.

Fig. 3. Habitats along the road transect in southern Quintana Roo, Mexico. The letters on the images correspond to those in Fig. 1.

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Starting on 13 February 2010, we have been conducting ongoing nocturnal surveys at 15 days intervals (i.e., every second Saturday) aboard an automobile moving at a speed of 40–50 km/h. The duration of each survey ranged from 3 to 5 h, depending on the frequency of sightings and the number of road-killed snakes recorded. The survey always has been conducted by PMBG, accompanied by various biology students and on some occasions by GK and JRCV. We recorded the following data for all the snakes encountered: the field number (with the initials of Pablo Beutelspacher García [PBG]); the species name; the date and time; the locality, with GPS coordinates obtained from a Garmin GPS device; the weather conditions (precipitation, wind, cloud coverage); and the condition of snake (alive, road-killed). The live snakes only were recorded and not preserved, except on a few occasions. All of the road-killed snakes were collected (except when the carcasses were decomposed or badly damaged) and placed in a plastic bag with a paper label containing the collecting information; after returning from the survey (the following morning at the latest) we preserved the collected snakes with an injection of absolute ethanol into the body cavity. For permanent maintenance, we transferred the specimens into 70% ethanol. We deposited one-half of the specimens in the collections of El Colegio de la Frontera Sur (ECOSUR), Chetumal, Quintana Roo, Mexico, the remaining at the Senckenberg Research Institute (SMF), Frankfurt am Main, Germany. We identified the snakes encountered in this study based on the keys in Köhler (2008). We provide an identification key to the species of snakes known or expected to occur in southern Quintana Roo. We examined all of the preserved specimens externally for a set of selected morphological (morphometric and scalation) characters. We determined their sex by inspecting the shape of the base of tail, the presence of hemipenes, and by direct inspection of the gonads. We also performed dissections to obtain data on the gonadal status and the possible presence of oviducal eggs (Köhler, 2016).

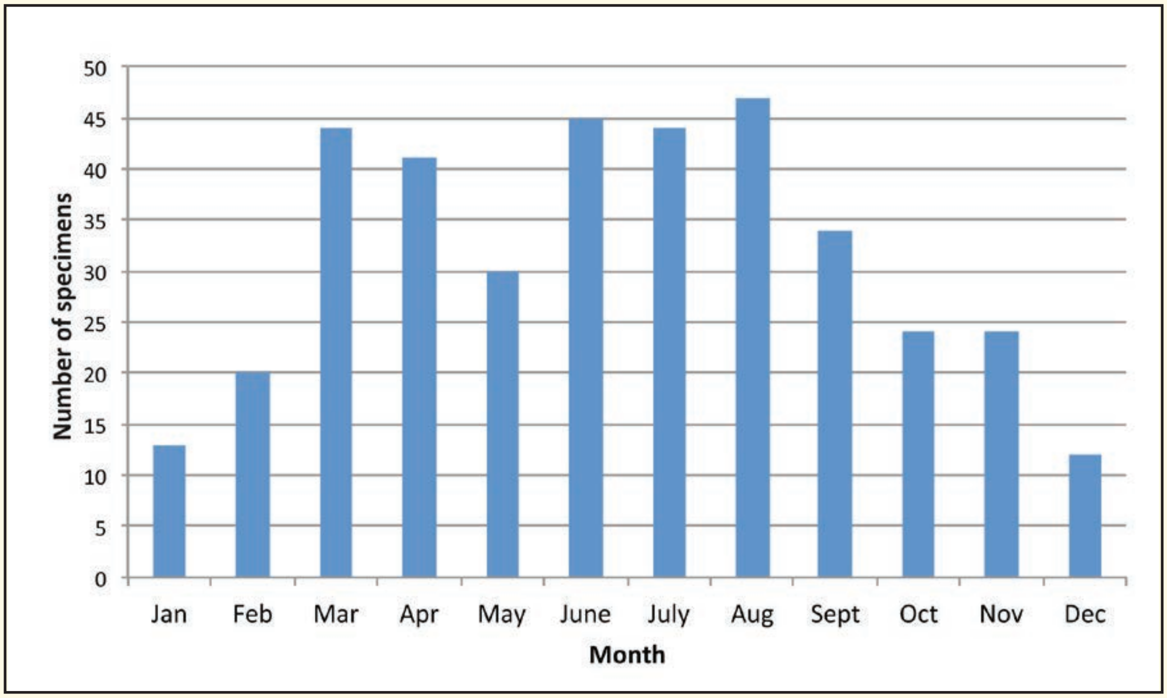

Fig. 4. Diagram showing the frequency distribution of collected road-killed snakes in the course of the year (average values calculated for the years 2010–2015).

To access the organs in the body cavity, we made a longitudinal cut along the ventral surface of the body. We then inspected the intestinal tract for obvious content before separating it from the rest of the body, which we opened via a longitudinal incision. We examined the intestinal contents for recognizable prey items, and once the intestinal tract and the liver were removed we inspected the gonads, which are situated dorsally near the vertebral column and anterior to the kidneys. We used digital calipers to measure the longitudinal and transverse diameters of each testis in males, and the longitudinal and transverse diameters of each ovary in females. We then examined the ovaries for the presence of previtellogenic and vitellogenic follicles, measuring the size of any vitellogenic follicles with calipers. If oviducal eggs were present, we determined the length and width of each egg and recorded the number of eggs separately for each oviduct.

RESULTS

As of 30 June 2016, our bi-monthly surveys generated a total of 578 snakes (433 road-killed, 145 alive), representing 31 species (Boidae: 1 species; Colubridae: 13; Dipsadidae: 13; Elapidae: 1; Natricidae: 1; Viperidae: 2; see Table 2). The number of road-killed snakes encountered per survey ranged from zero to 13 ($\bar{x} = 3.33$). Generally, we found more specimens during the summer months, which correspond with the rainy season, than during the dryer winter months (Figs. 4, 5). The total number of snakes collected per year was 121 (2010), 52 (2011), 65 (2012), 75 (2013), 70 (2014), and 60 (2015) ($\bar{x}$ = 73.83).

Table 2. Species list and frequency of recorded specimens from February 2010 to June 2016.

Family	Species	Collected	Sighted	Total
Boidae	*Boa imperator*	31	11	42
Colubridae	*Drymarchon melanurus*	1	4	5
	Drymobius margaritiferus	6	1	7
	Pseudelaphe flavirufa	6	0	6
	Ficimia publia	6	0	6
	Lampropeltis triangulum	10	1	11
	Leptophis ahaetulla	1	0	1
	Leptophis mexicanus	5	3	8
	Mastigodryas melanolomus	8	0	8
	Oxybelis aeneus	4	0	4
	Oxybelis fulgidus	5	2	7
	Spilotes pullatus	2	0	2
	Stenorrhina freminvillei	12	0	12
	Symphimus mayae	2	0	2
Dipsadidae	*Coniophanes imperialis*	21	3	24
	Coniophanes meridanus	7	0	7
	Coniophanes schmidti	12	1	13
	Dipsas brevifacies	86	14	100
	Imantodes cenchoa	2	0	2
	Imantodes tenuissimus	24	4	28
	Leptodeira frenata	41	4	45
	Leptodeira septentrionalis	1	0	1
	Ninia sebae	35	10	45
	Sibon nebulatus	1	0	1
	Sibon sanniolus	56	14	70
	Tretanorhinus nigroluteus	0	1	1
	Tropidodipsas sartorii	33	7	40
Natricidae	*Thamnophis proximus*	3	0	3
Elapidae	*Micrurus diastema*	21	4	25
Viperidae	*Bothrops asper*	36	6	42
	Crotalus tzabcan	7	3	10

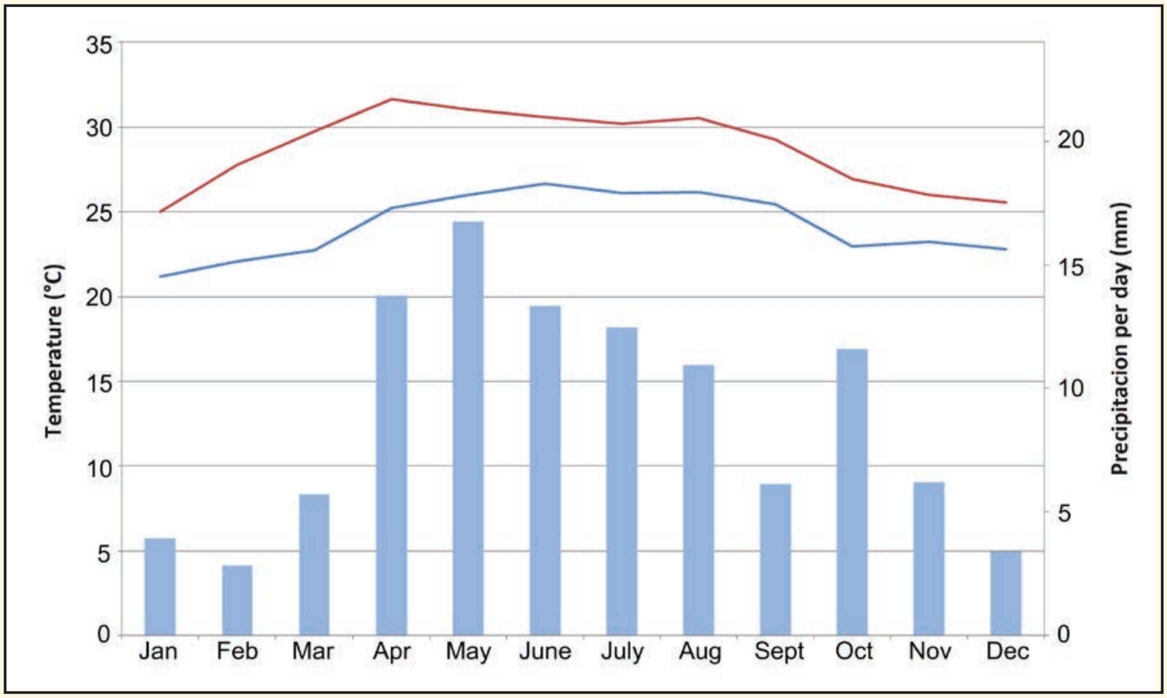

Fig. 5. Average daytime (red line) and nighttime (blue line) temperatures, and daily precipitation (blue vertical bars) at the study site. See text for details.

The most frequently recorded species were *Dipsas brevifacies* (100 specimens), *Sibon sanniolus* (70), *Leptodeira frenata* (45), *Ninia sebae* (45), *Boa imperator* (42), *Bothrops asper* (42), *Tropidodipsas sartorii* (40), *Imantodes tenuissimus* (28), *Micrurus diastema* (25) and *Coniophanes imperialis* (24) (Table 2). In a forthcoming series of articles, we will present data on the external morphology, seasonality, spatial distribution, reproduction, and diet for each of the species collected during these surveys, and in each article will provide data for several species.

Below we present an identification key to the snake species that are known or expected to occur in the Chetumal region. We marked species that are expected to occur in the region, but which we did not collect, with an asterisk.

Key to the Snakes of the Chetumal Region

1a Scales around body of equal size and shape (Fig. 6a); eyes not distinct, only indicated by dark spots . . . . ***Amerotyphlops microstomus****

1b Ventral scales much broader than dorsal body scales (Fig. 6b); eyes well-developed **2**

2a Ventral scutes narrow, not covering complete width of ventral body surface; dorsal scale rows at midbody more than 50 . . . . ***Boa imperator***

2b Ventral scutes covering complete width of ventral body surface; dorsal scale rows at midbody fewer than 30 . **3**

3a Head scales mostly irregular and in more than nine plates; a pair of erectile fangs in upper mouth **4**

3b Dorsum of head covered with nine symmetrical scutes; no pair of erectile fangs in upper mouth **6**

4a Tip of tail modified as a rattle . . . . *Crotalus tzabcan*
4b Tip of tail not modified as a rattle **5**

5a Snout covered with small irregular scales (Fig. 7a . . . . *Bothrops asper*
5b Snout covered with large symmetrical shields (Fig. 7b . . . . *Agkistrodon russeolus**

6a Dorsal scale rows at midbody in an even number (14–18); body black, usually with yellow blotches; total length to 2,600 mm . . . . *Spilotes pullatus*
6b Dorsal scale rows at midbody in an odd number; body pattern variable; total length variable **7**

7a Dorsal scale rows at midbody 15 . . . . **8**
7b Dorsal scale rows at midbody 17 or more **17**

8a Dorsal scale rows reduce to 11 one head length anterior to cloaca; cloacal scute divided **9**
8b No dorsal reduction: dorsal scale rows one head length anterior to cloaca 15; cloacal scute divided or entire **10**

9a No loreal scale, prefrontal in contact with supralabials (Fig. 8a . . . . *Leptophis ahaetulla*
9b Loreal scale present, separating prefrontal from supralabials (Fig. 8b . . . . *Leptophis mexicanus*

10a Cloacal scute entire **11**
10b Cloacal scute divided **13**

11a Body and tail with a distinct coral snake-like pattern of black and orange rings; no longitudinal mental groove . . . . *Dipsas brevifacies*
11b Body and tail without a distinct coral snake-like pattern of black and orange rings; longitudinal mental groove present **12**

12a First infralabials in contact with each other behind mental (Fig. 9a); 159–200 ventrals; 64–114 subcaudals; relatively stout-bodied snake, SVL to 596 mm . . . . *Sibon nebulatus*
12b First infralabials separated from each other by one postmental behind mental (Fig. 9b); 143–162 ventrals; 64–95 subcaudals; relatively slender snake, SVL to 386 mm . . . . *Sibon sanniolus*

13a More than 180 ventrals; 32–57 subcaudals; body pattern usually with complete black rings . . . . *Micrurus diastema*
13b Fewer than 170 ventrals; number of subcaudals variable; body pattern without complete black rings **14**

14a 150–165 ventrals; 115–146 subcaudals . . . . *Symphimus mayae*
14b 103–154 ventrals; 32–62 subcaudals **15**

15a 103–114 ventrals; 32–44 subcaudals . . . . *Tantillita canula**
15b 138–154 ventrals; 48–62 subcaudals **16**

16a Venter paler than dorsum; pale dorsal head band covers posterior end of parietals and the first 2–3 dorsal scale rows . . . . *Tantilla cuniculator**
16b Dorsum and venter uniformly dark brown to black; pale dorsal head band covers parietals and the first 2–7 dorsal scale rows . . . . *Tantilla moesta**

17a Dorsal scale rows at midbody 17 . . . **18**
17b Dorsal scale rows at midbody 19 or more . . . **33**

18a Dorsal scale rows reduce to 13 or 15 one head length anterior to cloaca. . . . **19**
18b No dorsal reduction: dorsal scale rows one head length anterior to cloaca 17. . . . **25**

19a At least some dorsal scales keeled . . . **20**
19b Dorsal scales smooth . . . **22**

20a Fewer than 160 ventrals; 103–138 subcaudals; dorsal scale rows reduce to 15 one head length anterior to cloaca . . . ***Drymobius margaritiferus***
20b More than 165 ventrals; 137–203 subcaudals; dorsal scale rows reduce to 13 one head length anterior to cloaca . . . **21**

21a Brown, gray or cream color in life and preservative; SVL to 1,455 mm . . . ***Oxybelis aeneus***
21b Green in life, blue in preservative; SVL to 2,000 mm . . . ***Oxybelis fulgidus***

22a Fewer than 140 ventrals; 78–90 subcaudals . . . ***Coniophanes meridanus***
22b More than 155 ventrals; number of subcaudals variable . . . **23**

23a Cloacal scute entire; 188–215 ventrals; 56–88 subcaudals. . . . ***Drymarchon melanurus***
23b Cloacal scute divided; 163–195 ventrals; 85–136 subcaudals . . . **24**

24a A subpreocular scale present below preocular scale (Fig. 10a); dorsal scale rows reduce to 13 one head length anterior to cloaca. . . . ***Masticophis mentovarius****
24b No small subpreocular scale present below preocular scale (Fig. 10b); dorsal scale rows reduce to 15 one head length anterior to cloaca . . . ***Mastigodryas melanolomus***

25a Cloacal scute entire. . . . **26**
25b Cloacal scute divided . . . **28**

26a Uniform black (adults) or red in life with pale neck band (juveniles . . . ***Clelia scytalina****
26b Body black with pale (white, yellow, or red in life) rings . . . **27**

27a Dorsal scales completely smooth; pale rings white, tan, or gray in life; body moderately compressed; eyes protruding . . . ***Tropidodipsas fasciatus****
27b Dorsal scales weakly keeled; pale rings yellow, orange, or red in life; body cylindrical; eyes non-protruding . . . ***Tropidodipsas sartorii***

28a Body extremely slender; head large and distinct from thin neck with large protruding eyes (Fig. 11a); 195–261 ventrals; 106–178 subcaudals . . . **29**
28b Head not conspicuously large, eyes normal (Fig. 11b); 173–217 ventrals; 137–203 subcaudals . . . **31**

29a Vertebral scale row distinctly enlarged (3–4 times as wide as adjacent scales; Fig. 12a); 228–261 ventrals; 134–178 subcaudals . . . ***Imantodes cenchoa***
29b Vertebral scale row not or only slightly enlarged (1.5–2.0 times as wide as adjacent scales; Fig. 12b); 195–262 ventrals; 106–155 subcaudals . . . **30**

30a Dark dorsal spots often interrupted at sides, especially posteriorly; 195–262 ventrals; 106–155 subcaudals . . . . ***Imantodes gemmistratus****

30b Dark dorsal spots not interrupted at sides; 241–254 ventrals; 142–158 subcaudals...***Imantodes tenuissimus***

31a Rostral shield protruding and pointed (Fig. 13a . . . . ***Ficimia publia***

31b Rostral shield normal (Fig. 13b **32**

32a Prenasal not fused with bordering internasal; anterior portion of body usually with coralsnake-like pattern; 132–166 ventrals; more than 100 subcaudals . . . . ***Scaphiodontophis annulatus****

32b Prenasal fused with bordering internasal (Fig. 13a); body longitudinally striped or unicolor, without coralsnake-like pattern; 160–182 ventrals; fewer than 50 subcaudals . . . . ***Stenorrhina freminvillei***

33a Cloacal scute entire **34**

33b Cloacal scute divided **38**

34a Dorsal scales smooth. **35**

34b Dorsal scales keeled **36**

35a Dorsal scales in oblique rows (Fig. 14a); 124–153 ventrals; body with blotches, no rings . . . . ***Xenodon rabdocephalus****

35b Dorsal scales in longitudinal rows (Fig. 14a); 205–244 ventrals; a body pattern of rings . . . . ***Lampropeltis triangulum***

36a Dorsal scale rows 15 or fewer one head length anterior to cloaca; 181–220 ventrals ***Phrynonax poecilonotus****

36b Dorsal scale rows 17 or more one head length anterior to cloaca; 130–181 ventrals **37**

37a No dorsal reduction: dorsal scale rows one head length anterior to cloaca 19; fewer than 75 subcaudals . . . . ***Ninia sebae***

37b Dorsal scale rows reduce to 17 one head length anterior to cloaca; more than 80 subcaudals . . . . ***Thamnophis proximus***

38a Dorsal scales keeled, at least on posterior body **39**

38b Dorsal scales smooth **41**

39a Fewer than 160 ventrals; fewer than 85 subcaudals . . . . ***Tretanorhinus nigroluteus***

39b More than 200 ventrals; more than 85 subcaudals **40**

40a Usually 8 supralabials, two bordering the eye (Fig. 15a); dorsal blotches, if present, brown or gray . . . . ***Senticolis triaspis****

40b Usually 9 supralabials, three bordering the eye (Fig. 15b); dorsal blotches reddish in life . . . . ***Pseudelaphe flavirufa***

41a Fewer than 150 ventrals **42**

41b More than 150 ventrals **43**

42a Dorsal scale rows at midbody 21; at outer portion of each ventral scale a large dark spot, such that a symmetrical row of spots runs along each ventral edge . . . . ***Coniophanes bipunctatus****

42b Dorsal scale rows at midbody 19; pattern on ventral scales not as described above . . ***Coniophanes imperialis***

43a Dorsal scale rows reduce to 19 one head length anterior to cloaca; body with longitudinal stripes; more than 81 subcaudals . . . . ***Coniophanes schmidti***

43b Dorsal scale rows reduce to 17 or fewer one head length anterior to cloaca; body patternless or with blotches, if with longitudinal stripes, then fewer than 81 subcaudals **44**

44a Pupils round; body patternless or with longitudinal stripes; 155–178 ventrals; 56–80 subcaudals . . . . ***Conophis lineatus****

44b Pupils vertically slit; body with blotches; 170–211 ventrals; 64–107 subcaudals **45**

45a One dark postorbital stripe present, in broad contact with first body blotch (Fig. 16a); a single dark spot in the center of each parietal; 170–192 ventrals; 64–86 subcaudals. . . . . ***Leptodeira frenata***

45b Dark postorbital stripe, if present, not in contact with first body blotch (Fig. 16b); markings on parietals not as described above; 174–211 ventrals; 72–107 subcaudals . . . . ***Leptodeira septentrionalis***

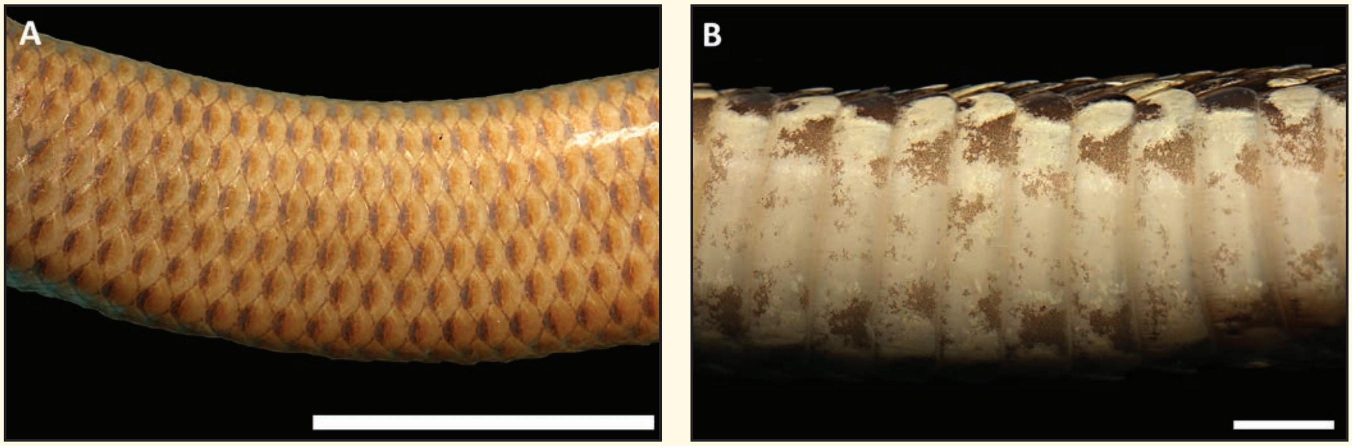

Fig. 6. Ventral body scales in (A) *Ramphotyphlops braminus* (SMF 74694); and (B) *Sibon nebulatus* (SMF 81283). Scales equal 5.0 mm.

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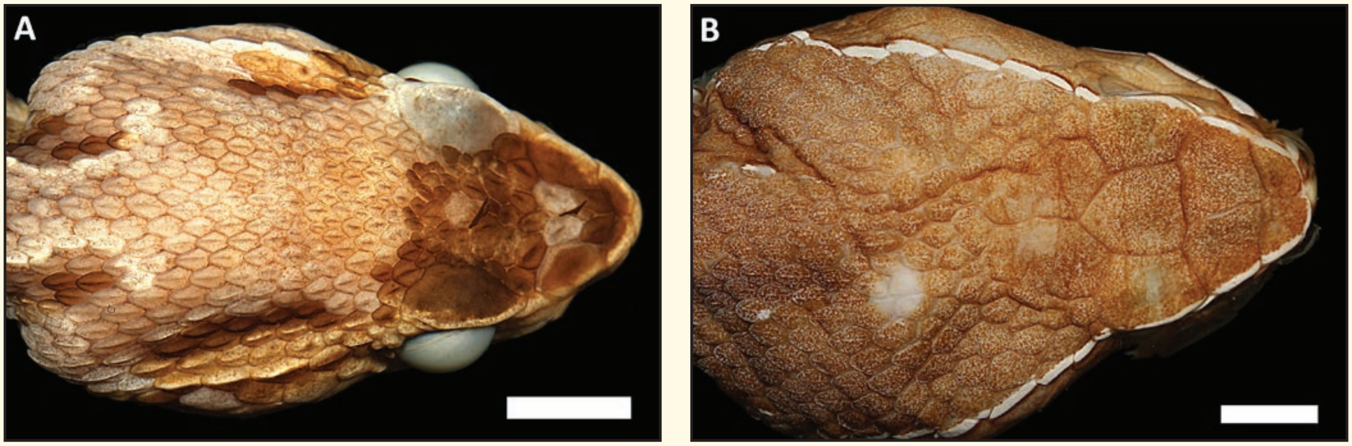

Fig. 7. Dorsal head scales in (A) *Bothrops asper* (SMF 79834); and (B) *Agkistrodon russeolus* (SMF 21090). Scales equal 5.0 mm.

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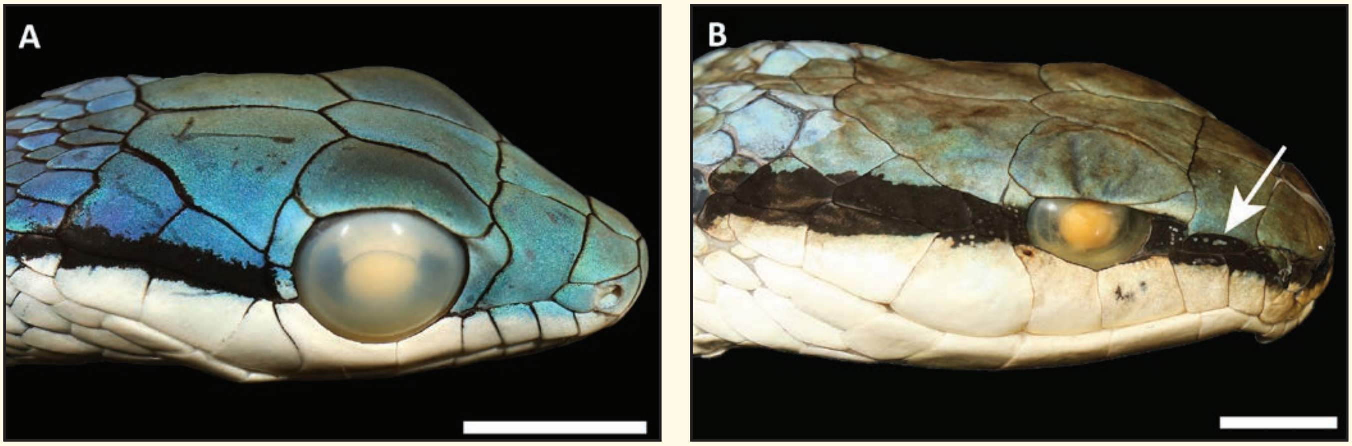

Fig. 8. Lateral head scales in (A) *Leptophis ahaetulla* (SMF 80834); and (B) *Leptophis mexicanus* (SMF 79563). Arrow points to loreal scale in *L. mexicanus*. Scales equal 5.0 mm.

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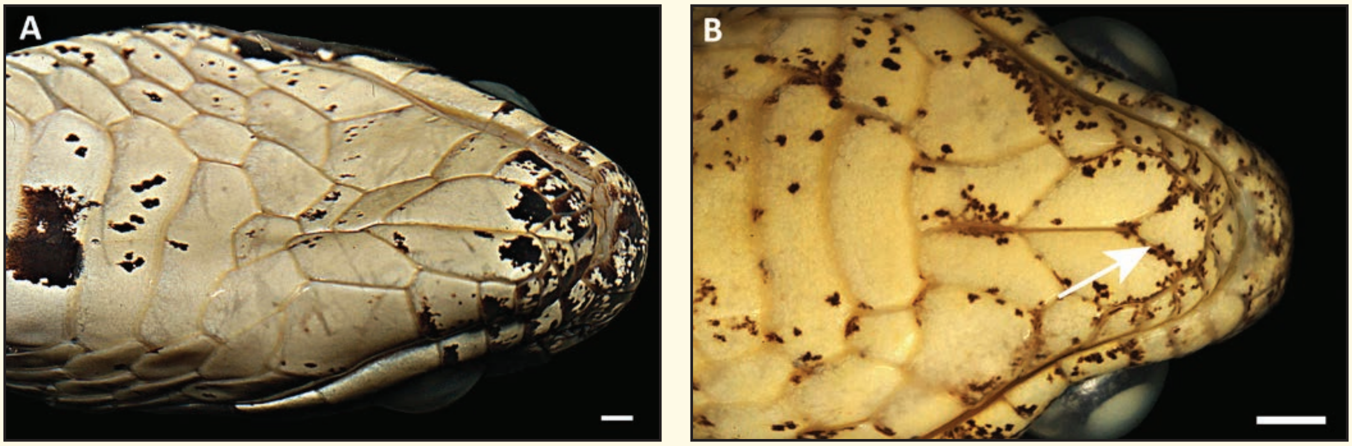

Fig. 9. Ventral head scales in (A) *Sibon nebulatus* (SMF 81283); and (B) *Sibon sanniolus* (GK-5161). Arrow points to postmental scale in *S. sanniolus*. Scales equal 5.0 mm.

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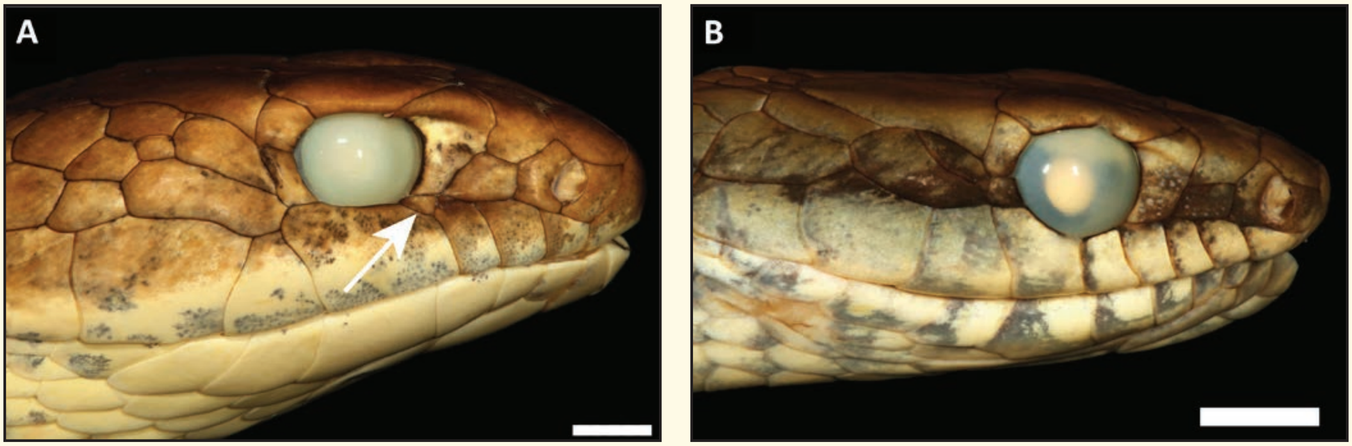

Fig. 10. Lateral head scales in (A) *Masticophis mentovarius* (SMF 79698); and (B) *Mastigodryas melanolomus* (SMF 77990). Arrow points to subpreocular scale in *M. mentovarius*. Scales equal 5.0 mm.

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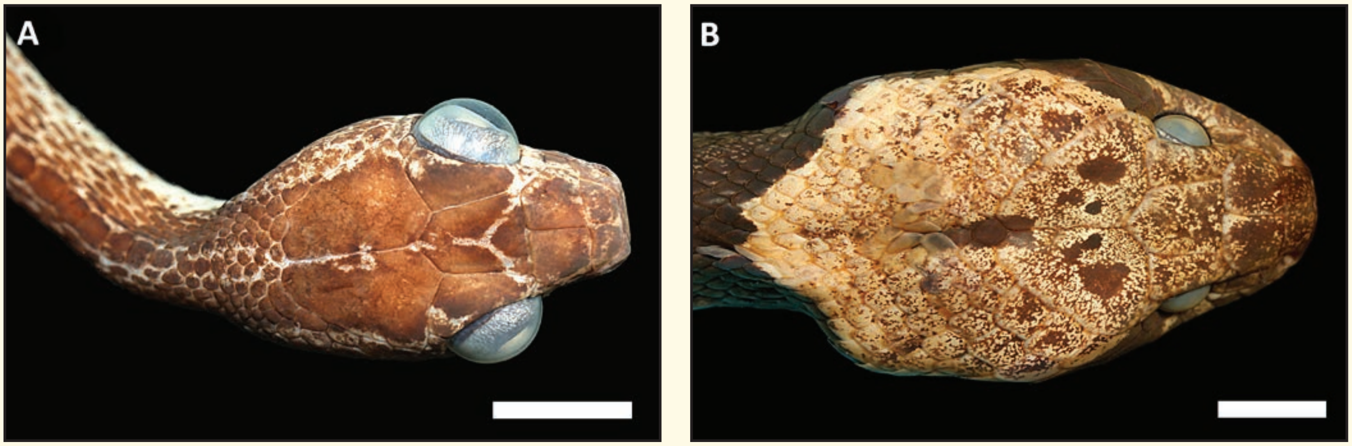

Fig. 11. Dorsal view of head in (A) *Imantodes cenchoa* (SMF 92068); and (B) *Leptodeira frenata* (SMF 68171). Scales equal 5.0 mm.

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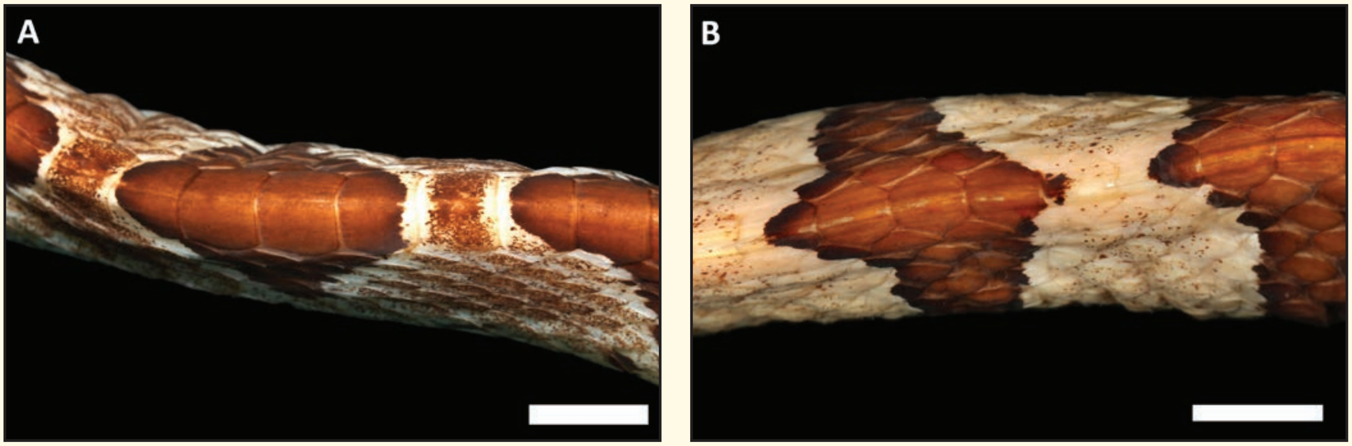

Fig. 12. Dorsal body scales in (A) *Imantodes cenchoa* (SMF 92068); and (B) *Imantodes tenuissimus* (SMF 68170). Scales equal 5.0 mm.

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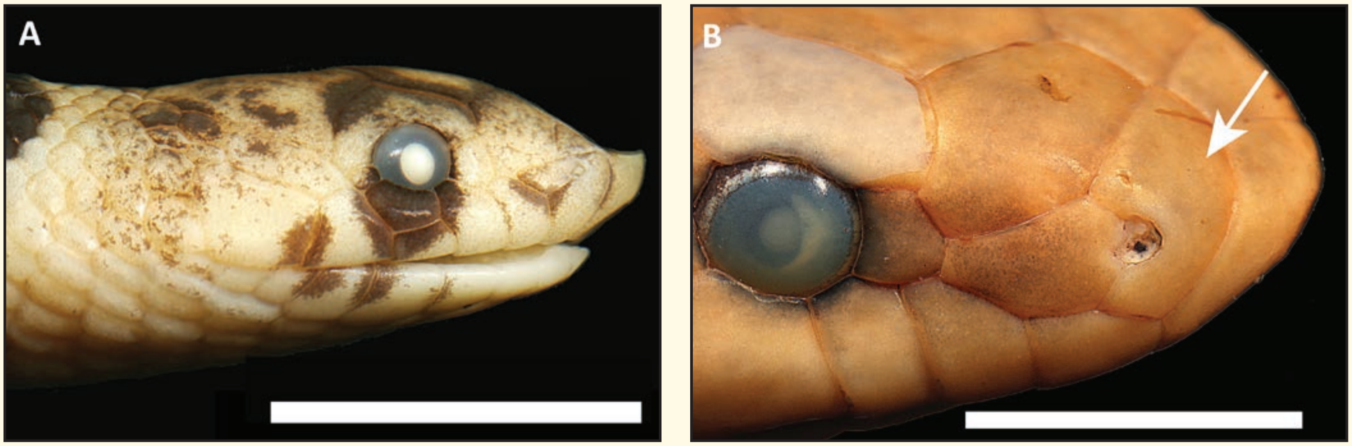

Fig. 13. Lateral view of head in (A) *Ficimia publia* (SMF 79878); and (B) *Stenorrhina freminvillei* (SMF 84786). Arrow points to fused prenasal-internasal scale in *S. freminvillei*. Scales equal 5.0 mm.

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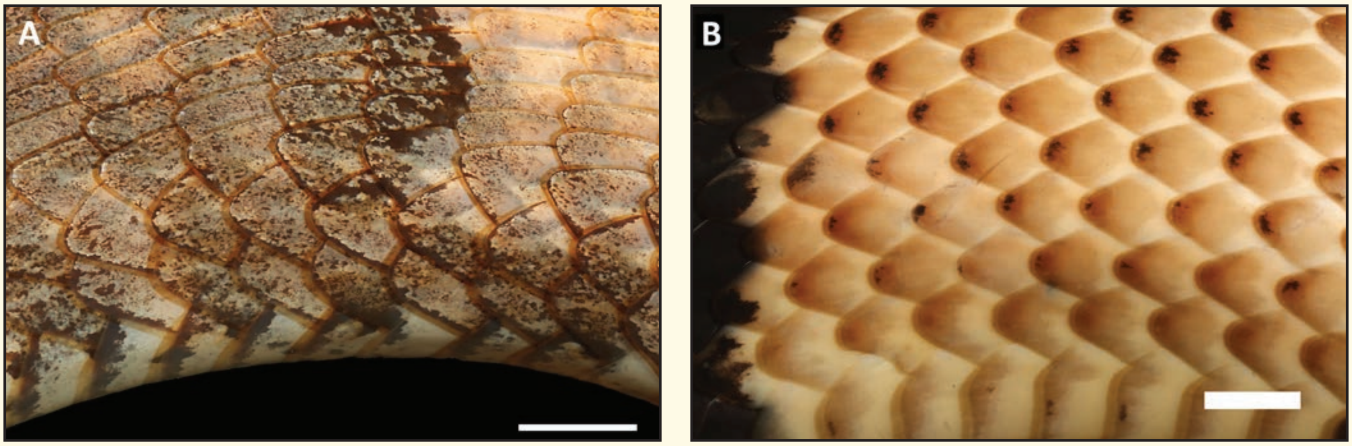

Fig. 14. Dorsal body scales in (A) *Xenodon rabdocephalus* (SMF 90957); and (B) *Lampropeltis triangulum* (SMF 98942). Scales equal 5.0 mm.

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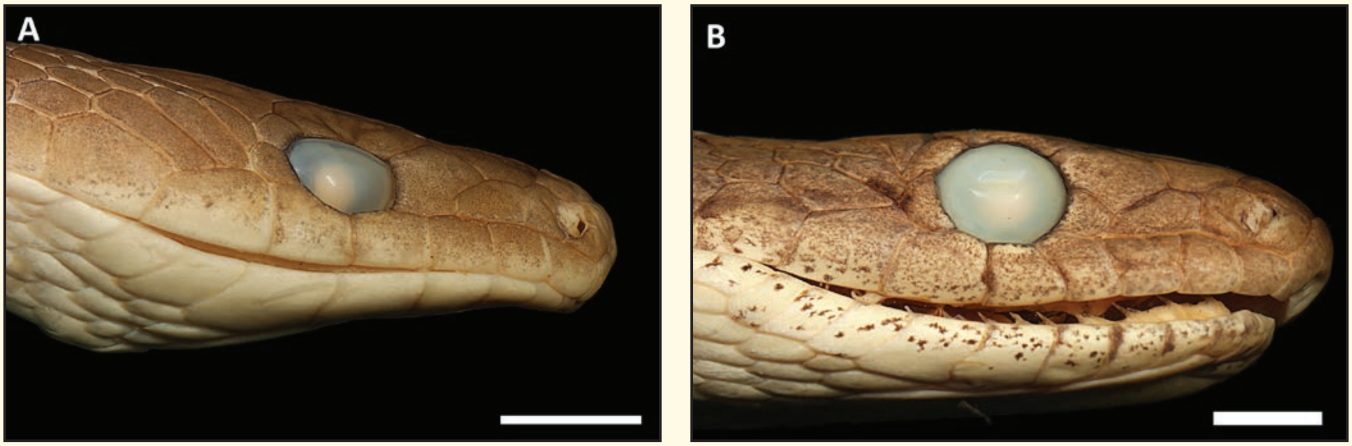

Fig. 15. Lateral view of head in (A) *Senticolis triaspis* (SMF 81282); and (B) *Pseudelaphe flavirufa* (SMF 79332). Scales equal 5.0 mm.

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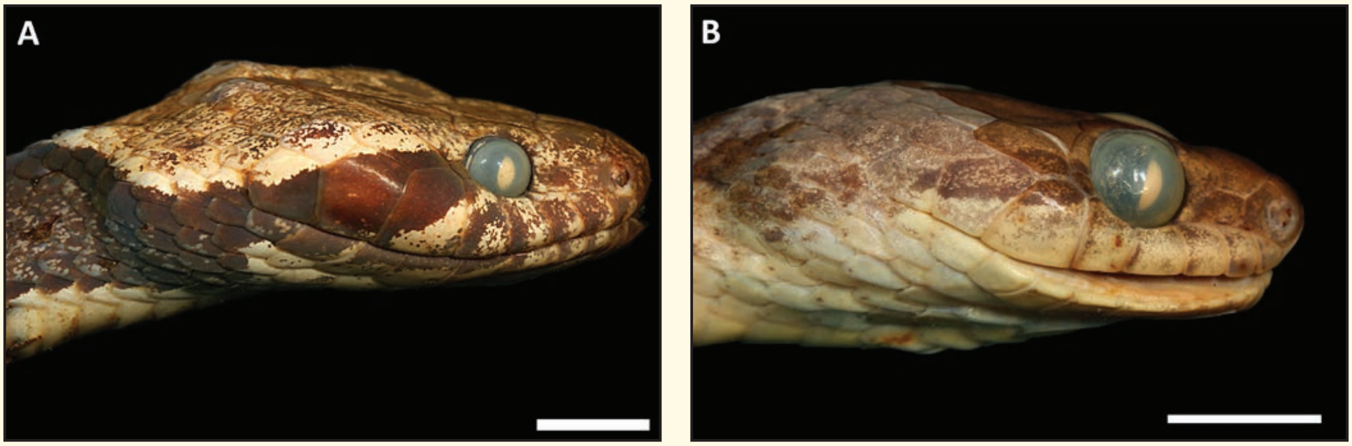

Fig. 16. Lateral view of head in (A) *Leptodeira frenata* (SMF 68171); and (B) *Leptodeira septentrionalis* (SMF 86054). Scales equal 5.0 mm.

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DISCUSSION

Road-killed specimens can be an excellent source of material for studies on the reproduction, diet, or population dynamics of snake species (Köhler, 2016). An advantage of such studies is the fact that the individuals used already were dead when collected. Relying on road-killed specimens also has a disadvantage, however, because the condition of the collected specimens can vary considerably, depending on how long a specimen has been dead before preservation, as well as how badly it has been damaged (from the impact of vehicles, and from scavengers such as ants). The latter observation leads to a relevant question: How long do the bodies of road-killed animals remain on a road before scavengers take them? Among the factors that influence the accuracy of estimates, the time of carcass persistence has been considered as one of the most important factors inducing bias in road mortality estimates (Coelho et al., 2008). The available studies that addressed this question indicate that snake carcasses persisted on the road for usually less than one day after being killed by a vehicle (Santos et al., 2011). It seems safe to assume, therefore, that the specimens collected during a single survey were killed the same day, and not days earlier. The rapid and intense removal of road-killed animals by scavengers indicates an actual risk for underestimating snake mortality. Ideally, studies that use data from road-killed snakes to study the impact of traffic on snake populations would benefit from a concurrent investigation of carcass persistence and the application of appropriate correction factors to attain realistic estimates of snake mortality (Degregorio et al., 2011).

In a review, Colino-Rabanal and Lizana (2012) concluded that increasing vehicular traffic is widely suspected to compromise herpetofaunal conservation and to play a role in population declines; they also stated that the research on road impacts on populations is fragmented, and can be contradictory due to differences in the methodology. In this regard, in term of road mortality rates, only a few studies reporting road-killed snakes were comparable with our study (Table 3).

Table 3. Comparison of our study with other works that present snake Road Mortality Rates (RMR).

Location	Transect distance (km)	Period (No. Trips)	No. Species	No. Road-killed Snakes	RMR (ind/km/day)	Reference
SE Quintana Roo, Mexico	39	February 2010–June 2016 (177)	31	433	0.06	This study
Australia	77	August 2009–July 2010 (77)	15	34	0.0057	McDonald (2012)
Western Colombia	2.4	February–July 2006 (176)	9	35	0.047	Vargas-Salinas et al. (2011)
Isthmus of Tehuantepec, Mexico	1.2	14 September–20 November 2007 (49)	—	34	0.57	Grosselet et al. (2008)
Western Louisiana, United States	128	March–June 1948 (37)	17	66	0.014	Fitch (1949)
Western Kansas, United States	416	One day (1)	8	57	0.13	Bugbee (1945)

GK, who joined PMBG on several surveys, was impressed with PMBG's skills to detect snakes—even very small individuals—on the road while driving some 50 km/h. Some researchers have argued that surveys on foot are more effective than on a vehicle (Enge and Wood, 2002; Slater, 2002), but because of greater costs in terms of time and manpower, foot surveys would not have been feasible for our project.

As we have shown in this article (and in the ones that will follow), long-term studies based on road-killed animals resulting in a meaningful series of individuals for inclusion in projects on natural history, internal anatomy, external morphology, and on the evolutionary biology of reproduction are possible to design.

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