Are tropical reptiles really declining? A six-year survey of snakes in Drake Bay, Costa Rica, and the role of temperature, rain and light

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Abstract: Introduction: studies in the last two decades have found declining snake populations in both temperate and tropical sites, including informal reports from Drake Bay, Costa Rica. **Objective:** to investigate if reports of decreasing snake populations in Drake Bay had a real basis, and if environmental factors, particularly temperature, rain and light, have played a role in that decrease. **Methods:** we worked at Drake Bay from 2012 through 2017 and made over 4000 h of transect counts. Using head flashlights we surveyed a transect covered by lowland tropical rainforest at an altitude of 12–38 m above sea level, near the Agujas River, mostly at 1930–2200 hours. We counted all the snakes that we could see along the transect. **Results:** snake counts increase from August to September and then decline rapidly. The May snakes/rainfall peaks coincide, but the second snake peak occurs one month before the rain peak; we counted more snakes in dry nights, with the exception of *Imantodes cenchoa* which was equally common despite rain conditions. We saw less *Leptodeira septentrionalis* on bright nights, but all other species were unaffected. Along the six years, the number *of species* with each diet type remained relatively constant, but the number *of individuals* declined sharply for those that feed on amphibians and reptiles. We report *Rhadinella godmani*, a highland species, at 12–38 m of altitude. **Conclusion:** night field counts of snakes in Drake Bay, Costa Rica, show a strong decline from 2012 through 2017.

Key words: snake demography, moonlight, rain, temperature, climate change in Osa.

Total Words: 3908

Snakes are particularly susceptible to population decline because of their long life spans, late sexual maturity, low reproductive frequency, site fidelity and significant mortality among neonates and juveniles (Scott & Seigel, 1992; Shetty & Shine, 2002). They are also good ecological indicators because their populations often reflect fluctuations in the environment and in the populations of their prey (Moore et al., 2003; Madsen, Ujvari, Shine, & Olsson, 2006).

Population status assessments are difficult because of their cryptic life styles and low or sporadic activity (Gibbon et al., 2000), but there have been reports of population decline in temperate regions, including the United States of America (Mount, 1975; Rudolph & Burgdorf, 1997; Conant & Collins, 1998; Hallam, Wheaton, & Fischer, 1998; Tuberville, Bodie, Jensen, LaClaire, & Gibbons, 2000; Winne, Willson, Todd, Andrews, & Gibbons, 2007) and Europe (Reading et al., 2010). The situation may be worse in the tropics, where documented studies are even more scarce (Böhm et al., 2013; Urban, 2015): declines include the extinction of the Round Island Burrowing Boa, endemic to Mauritius (Bullock, 1986; Greene, 2000), and population

drops of snakes in Nigeria (Reading et al., 2010) and Australia (Lukoschek, Beger, Ceccarelli, Richards, & Pratchett, 2013; Lukoschek, 2018).

Even though snake declines seem to be a reality in many parts of the world, hundreds of samples are needed to detect real declines (Kery, 2002; Sewell, Guillera-Arroita, Griffiths, & Beebee, 2012; Hileman et al., 2018). Furthermore, problematic assumptions used in mathematical models can lead to suspicious conclusions (e.g. exaggerated extinction rate estimates: McCallum, 2007).

Reports of snake declines are frequently based on anecdotal evidence and there is a need for studies that provide intensive counts for prolonged periods (Krysko, 2001; Böhm et al., 2013; Urban, 2015); for example, local tourist guides in Drake Bay, Costa Rica, have told us that populations have been declining for nearly two decades. Our objective in this study was to investigate if their impression is matched by more formal data collection.

MATERIALS AND METHODS

We worked at Drake Bay, South Pacific of Costa Rica (N 08.69420–08.69490; W 083.67421–083.67495), from 2012 through 2017, and made over 4 000 h of transect counts of snakes. These counts were made while we were accompanied by small groups of tourists as part of our work as field guides in the area.

We hypothesized that climate changes may reduce local populations of some species and increase others; and that snakes that feed exclusively on amphibians or insect prey (which fluctuate strongly with rain or temperature), should be more affected than generalist species.

Snake counts: Using head flashlights we surveyed a transect covered by lowland tropical rainforest, 12–38 m above sea level, near the Agujas River (Fig. 1 in Digital Appendix 1). We counted all the snakes that we could see along the transect; identified them *in situ* (guides by Savage, 2002 and Solórzano, 2004), and photographed them for taxonomic corroboration (Digital Appendix 2). We worked mostly from 1930 to 2200 hours, but a few counts started at 1730 and ended at 2245 hours (sampling hours per date in Digital Appendix 2).

Precipitation rates and temperature: Precipitation rates and temperature data were kindly provided by the *Instituto Meteorológico Nacional de Costa Rica* from the nearest meteorological station at Rancho Quemado.

Note: Rancho Quemado, where the meteorological station is located, has an altitude of 240 m above sea level while the survey site in Drake Bay has an altitude of 12 to 38 m, so we expected a difference in temperature between the study site and the meteorological station. To assess this difference, we made temperature measurements directly in Drake Bay from February 2017 to August 2017 and compared them with Rancho Quemado for that same time period. We found that average temperatures in Drake Bay are 2 to 3 degrees Celsius higher than temperatures in Rancho Quemado, but that *the trends along the timeline are the same*. No precipitation records were available from January 2012 to July 2012, December 2016 to March 2017 and September 2017 to December 2017. No temperature records were available from January 2012 to July 2012 and from September 2017 to December 2017.

Moon and *in situ* rain: Instead of using published moon phase data, we recorded moonlight conditions on every trip directly in the trail because cloudy skies produce dark nights

even when the moon is full. We used both official rain records and our own classification of rain condition during the trip (see Results).

Statistical analyses: We analyzed the counts independently for each of the most common species, and pooled the rare species into an "others" category that we also analyzed (Table 2 and Table 3 in Digital Appendix 1).

Ethical, conflict of interest and financial statements: the authors declare that they have fully complied with all pertinent ethical and legal requirements, both during the study and in the production of the manuscript; that there are no conflicts of interest of any kind; that all financial sources are fully and clearly stated in the acknowledgements section; and that they fully agree with the final edited version of the article. Tracie L. Stice and Gianfranco Gómez collected the data, Jose Pablo Barquero-González and Julián Monge-Nájera analyzed the data, all the authors participated in writing the manuscript. We did not need collecting permits because we did not collect any animals. A signed document with this statement has been filed in the journal archives.

<div align="center">RESULTS</div>

Species observed: In total, we recorded 25 snake species, representing five families (Boidae, Colubridae, Dipsadidae, Elapidae, Viperidae) (Table 1 in Digital Appendix 1).

Effect of diet: Along the six years, the number of species with each diet type remained relatively constant, fluctuating by a couple of species each year (Fig. 2 in Digital Appendix 1). However, the numbers of individuals changed visibly along the six-year study period depending on their main diet items. Species that mostly eat fish and invertebrates were always rare, and thus insufficient for us to see temporal trends; snakes that mostly feed on birds and mammals, which had larger populations, declined from 2012 through 2015. Finally, species that feed mostly on reptiles and amphibians were initially abundant but also have constantly declined over the six-year period, despite some occasional population peaks (Fig. 3 in Digital Appendix 1).

Annual patterns: When we compared counts of the five most frequent species with rainfall and temperature during the six-year study period, we noticed several trends (Fig. 4 in Digital Appendix 1). One is a weak increase in overall temperature along the study period. The other is that numerically dominant species have highly specific patterns but most started a decline since 2015. We observed a decrease in *L. septentrionalis* and *I. cenchoa* since 2015; *E. sclateri* is scarce (except for a peak from August to September of 2012 and 2014) but it has become even rarer since 2015; *S. compresus* was not seen after April 2016; finally, *M. melanolomus* had no clear tendency to grow or decline from 2012 to 2017, but showed a peak between August to September (Fig. 4 in Digital Appendix 1).

Monthly pattern: Mean temperature does not change strongly along the year, but rainfall increases after February and reaches a maximum in October, while snake counts increase from August to September and then decline rapidly. The May snakes/rainfall peaks coincide, but the second snake peak occurs one month before the rain peak (Fig. 5 in Digital Appendix 1).

Ecological correlations: The statistical significance values of ANOVA tests appear in Table 2 and Table 3 (Digital Appendix 1) and the counts/environmental condition relationships in the appendices,

Effect of rain*:* We counted more snakes in dry nights, with the exception of *I. cenchoa* which was equally common despite rain conditions (Fig. 6 in Digital Appendix 1).

Effect of moonlight*:* We saw less *L. septentrionalis* on bright nights, but all other species were unaffected so they are not presented in the figure (Fig. 7 in Digital Appendix 1).

Final considerations*:* We did not see differences in leaf litter quantity from the beginning to the end of the study period (Digital Appendix 2). Our finding of *R. godmani* is unexpected because it is a highland species (see Discussion).

DISCUSSION

Food*:* Snake activity patterns depend on changes in food availability throughout the year (Henderson, Dixon, & Soini, 1978; Martins, 1994). Snake species that ambush their prey and rely on sit-and-wait strategies are particularly susceptible because of their low rate of food acquisition (Webb & Shine, 1998), just like specialist species, which are less likely to exploit alternative resources in response to shifting environmental conditions (Terborgh & Winter, 1980; Gaston, 1994). Counts of *I. cenchoa*, a snake that feeds mainly on reptiles, sharply fell in 2015 and 2017; *E. sclateri*, a specialist feeder on reptile eggs, declined in 2015 and almost disappeared in 2016–2017, possibly due to scarce prey. The fall in the numbers of *L. septentrionalis* matches the fall in the abundance of prey species like *Boana rosenbergi, Smilisca phaeota* and *Agalychnis callidryas*; nevertheless, other prey items for this species, like *Rhinella horribilis* and *Craugastor fitizingeri*, remained common (Gianfranco Gómez, personal observation).

If we consider that four of the five species affected by rainfall in our study have diets consisting primarily of amphibians, reptiles, or both, our results are consistent with those of a study in Mexico, where more rain lead to more amphibian activity and to increased populations of the snakes that feed on them (Duellman, 1958).
Rhadinella godmani is a small leaf litter snake of uncertain diet and considered a highland species (Savage, 2002; Solórzano, 2004); we ignore if its presence at near sea level in Drake is in any way related to changes in environmental factors.

Temperature: Higher temperatures reduce the metabolic rate of snakes and restrain their activity and visibility (Seigel, Collins, & Novak, 1987; Zamora-Camacho, Moreno-Rueda, & Pleguezuelos, 2010; Rugiero, Milana, Petrozzi, Capula, & Luiselli, 2013). In Drake Bay, average monthly temperatures did not vary widely, so we are not surprised that there were no strong, generalized trends in species abundance that could be related with temperature. This matches previous work with tropical species (e.g. Shine & Madsen, 1996; Luiselli & Akani, 2002). Only one species, *S. compressus*, which needs fresh, shady habitats, was not recorded at all from our sampling site along 2016 and 2017.

Rain*:* There are reports of no correlation between counts of Neotropical snakes and rainfall (Henderson & Hoevers, 1977; Martins, 1994; Bernarde & Abe, 2006) and this is similar to our finding that the arboreal *I. cenchoa* was equally common despite rain conditions. Other species become more active with rain (Daltry, Ross, Thorpe, & Wüster, 1998; Oliveira &

Martins, 2001; Morrison & Bolger, 2002), but we did not see any species more often in rainy nights in Drake, quite the opposite, Drake snake counts were higher in dry nights. Perhaps they avoid the cold rainwater (rain is cold in the tropics, too).

Moonlight: Snakes may increase activity in full moon nights, when prey are more visible (Lillywhite & Brischoux, 2012; Connoly & Orrock, 2018); for example, the tropical tree snake *Boiga irregularis* even moves to areas where moonlight is stronger (Campbell, Mackessy, & Clarke, 2008). However, *Crotalus viridis* avoids bright moonlight, possibly to escape detection by its predators (Clarke, Chopko, & Mackessy, 1996). In our study, the fewer sightings of *L. septentrionalis* on nights with strong moonlight may also mean that it is avoiding predation, but we saw all the other species at Drake with the same frequency in dark and illuminated nights.

Final remarks: The clear decline in snake counts at Drake along the years might mean that their populations have decreased, that they moved out of sight or that they migrated to higher, cooler areas. They did not seem to avoid the transect because of our presence there (actually a few species remained constant in our counts along the years) and we do not think they found a suitable habitat at higher altitude because of human alteration of habitats around the reserve. We believe that the population decline in Drake is real and needs attention from the conservation authorities.

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RESUMEN

¿Están disminuyendo los reptiles tropicales? Seis años de monitoreo en las serpientes de Bahía Drake, Costa Rica, y el papel de la temperatura, la lluvia y la luz. Introducción: los estudios realizados en las últimas dos décadas han encontrado una disminución de las poblaciones de serpientes en ecosistemas templados y tropicales, incluyendo observaciones informales en Bahía Drake, Costa Rica. **Objetivo:** investigar si los informes de disminución de las poblaciones de las serpientes de Bahía Drake tuvieron una base real, y si los factores ambientales, particularmente temperatura, lluvia y luz, han jugado un papel en esa disminución. **Métodos:** trabajamos en Bahía Drake desde el 2012 hasta el 2017 y realizamos más de 4 000 h de recuentos de serpientes. Usando linternas de cabeza y en un horario mayormente entre las 1930 y las 2200 horas, examinamos un transecto de bosque tropical de bajura a 12–38 m.s.n.m, cerca del río Agujas. **Resultados:** la cantidad de serpientes vistas aumenta de agosto a setiembre y luego disminuye rápidamente. Los picos de serpientes y lluvia coinciden en mayo, pero el segundo pico de serpientes es un mes antes del pico de lluvia; contamos más serpientes en las noches secas, con la excepción de *Imantodes cenchoa* que era igualmente común en todas las condiciones de lluvia. Vimos menos *Leptodeira septentrionalis* en noches brillantes, pero las demás especies no se vieron afectadas por la luz lunar. A lo largo de los seis años, la *cantidad de especies* con cada tipo de dieta se mantuvo relativamente constante, pero la *cantidad de individuos* disminuyó considerablemente en las especies que se alimentan de anfibios y reptiles. Hallamos *Rhadinella godmani,* una especie de montaña, a 12–38 m de altitud. **Conclusión:** los

conteos nocturnos de serpientes en Bahía Drake, Costa Rica, muestran una fuerte disminución del 2012 al 2017.

Palabras clave: demografía de serpientes, luz de la luna, lluvia, temperature, cambio climático en Osa.

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