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Demographic analysis of snake killing as a conservation threat: *study case for a population of Ninia atrata*

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Análisis demográfico de la matanza de serpientes como amenaza para su conservación: estudio de caso de una población de *Ninia atrata*

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Dedicado a:

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Symbol	Term	Unit SI	Definition
$T°$	Temperature	celsius	*DF*
t	Time	s	*DF*
V	Volume	m^3	$\int dr^3$
X^2	Chi-square test		$X^2 = \sum_{i=1}^{h}\sum_{j=1}^{k}\frac{(O_{ij}E_{ij})^2}{E_{ij}}$
λ	Asymptotic growth		Eventual population growth rate
w	Stable distribution		The post-transient proportion in each class (age or stage)
v	Reproductive value		Mean number of offspring produced from a post-transient individual in each class

Abbreviation term

AIC	Akaike information criterion
CJS	Cormack-Jolly-Seber
CMR	Capture- marked recapture
Co	Covariate
H	Kruskal-Wallis tests
HSEQ	Health, Safety, Environment and Quality
IPM	Integral projection model
MPMs	Matrix Population Model
SSK	sexual segment of the male kidney
P	Probability value
SVL	Snout-vent length
sd	Standard deviation
TL	Tail length
Var	Variable
W	Wilconxon test

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2. Resumen

A nivel mundial, la matanza intencional de serpientes ha sido reconocida como una de las causas de extinción de sus poblaciones. Sin embargo, los efectos esta fuente de mortalidad han sido poco estudiados, haciendo que las estrategias de conservación que buscan mitigar esta amenaza sean poco efectivas. Esta tesis doctoral tiene como objetivo principal evaluar los efectos demográficos derivados de la matanza intencional de serpientes. Se empleó una población de la especie *Ninia atrata* como estudio de caso para evaluar la hipótesis que indica que la matanza intencional de serpientes tiene un impacto profundo en la viabilidad de las poblaciones de serpientes. Para este ello, se emplearon modelos de proyección integral (MPI) como aproximación metodológica para el modelamiento demográfico de la población de estudio. El efecto de la matanza intencional se estudió por medio de análisis perturbaciones frente a diferentes escenarios de matanza de serpientes. Para construir las tasas vitales empleadas en el modelo demográfico, se llevó a cabo una exploración profunda de los rasgos de la historia natural de *Ninia atrata*. Particularmente, se describió en detalle la relación entre la fenología reproductiva, la ecología de la alimentación y las interacciones presa-depredador con factores bióticos y abióticos tales como la variabilidad climática, la estacionalidad y la disponibilidad de alimentos. Como resultado, quedó claro que el patrón de la matanza intencional de serpientes en un paisaje agrícola puede predecirse a partir de las tareas desarrolladas por los campesinos. Sin embargo, este patrón se ve afectado por factores subyacentes como la forma en que los trabajadores de campo experimentaron el miedo, el género y nivel educativo de los trabajadores del campo. El reclutamiento y la fecundidad fueron los principales procesos demográficos que impulsan la trayectoria de la población de *Ninia atrata* bajo estudio, indicando que esta población es de vida corta con una dinámica poblacional que se inclina hacia el extremo rápido del continuo "rápido-lento" dentro del patrón de estrategias de historia de vida. En consecuencia, la matanza intencional de serpientes no representa una amenaza significativa para su viabilidad poblacional. Esto sugiere que las especies de serpientes tropicales de vida corta presentan una baja vulnerabilidad ante esta amenaza. No obstante, la variabilidad climática extrema y la pérdida de la calidad de hábitat representan amenazas significativas para sus poblaciones.

3. Abstract

Intentional killing has recognized worldwide as one of the causes of snake populations decline. However, the effects of intentional killing have been poorly studied, as well as conservation and management initiatives devoted to mitigate this threat. This doctoral thesis concerns about the demographic effects derivate from intentional snake killing on wild populations. Therefore, a population of the species *Ninia atrata* was employed as study case to evaluate hypothesis that the intentional snake killing has deep impact in the viability of populations. For this purpose, a population dynamic of *Ninia atrata* population that inhabit at oil palm plantation was modeled using an integral projection models (IPM) as demographic approach. Afterwards, the demographic responses of the model in front of different killing snake scenarios were assessed. To build the vital rates employed in the demographic model, a deep exploration of the *Ninia atrata* natural history traits was carried out. Particularly, the relationship between reproductive phenology, feeding ecology, and prey-predator interactions with biotic and abiotic factors such as climatic variability, seasonality, and food availability, were described in detail. As a result, it was clear that the pattern of intentional snake killing on agricultural landscape can be predicted from tasks developed by field workers. However, this pattern is affected by underlying factors such as the way in which field workers experienced fear, gender and educational level, rather than seasonality or climatic variability on snake abundances or richness. Besides, the population structure of the species is mainly composed by neonates, with a significant seasonal variability. Apparent survival rate showed a negative relationship with body mass suggesting that as the snake body mass increases, the chances of survival decreases. Recruitment and fecundity were the main demographic processes driving the population fate, in which heavy weighted snake individuals have the strongest contribution to long-term population size. Finally, the perturbation analyses showed that the intentional snake killing does not represent a significant threat to the viability of the *Ninia atrata* population under study. This suggests that short-lived tropical snake species with a fast life history strategy allocating a high reproductive effort at each of its few reproductive occasions are able to escape from this source of mortality.

4. General introduction

The human-snake conflict goes back from the caveman´s legacy in which humanity began to name its fears and threats. Currently, the human-snake conflict focuses on rural or suburban areas because a high portion of the population lives in urban areas and they have never seen a snake in their daily lives (Dood, 1987). Human attitudes toward snake have ranged from fascination, awe, and worship to fear and loathing (Morris & Morris, 1965). Certainly, the latter attitude is prevalent in many countries today, provoking a significant anthropogenic mortality of snakes in most wild populations (Bonnet, et al., 1999, Burghardt, et al., 2009). Worldwide, there are ten recognized threats that derive from human-snake conflict that contribute to the decline of snake's populations such as: commercial hunt, magic-religious hunt, pollution, intentional killing, road killing, habitat loss, climate change, invasive species, cascading declines, and infection diseases (e.g. *Ophidiomyces ophiodiicola*) (Dood, 1987, Row, *et al.,* 2007, Todd *et al.,* 2010, Bishop, *et al.,* 2016, Lorch, *et al.,* 2016).

Particularly, the snake unsustainable removal from natural populations has been well-defined in human behaviors such as economic profit (commercial hunting), feeding (survival hunting), spiritual benefit (magic-religiuos hunting), health profit (medicine), fear (psychological or cultural aversion), and accidental killing (vehicular traffic, agricultural machinery, among others) (Bonnet, Naulleau, & Shine, 1999; Todd, Wilson, & Gibbons, 2010; Godley & Moler, 2013, Osorno-Muñoz, *et al.,* 2014). Despite the clear identification of the sources of snake mortality, knowledge about the conservation status of snake species at the global level is rudimentary due to the lack of rigorous and comparable studies (Dood, 1987; Seigel and Mullin, 2009).

In a similar manner, sources of snake mortality in Colombia have been poorly studied. Few studies have quantified the number of animals killed annually by activities other than human consumption or livelihood hunting (Osorno-Muñoz, *et al.,* 2014). Recently, Lynch (2012) indentified five threats for snake populations in Colombia: habitat loss, intentional killing by field workers and peasants, illegal trafficking of species, road killing and scientific surveys (Vargas-Salinas, *et al.,* 2011). Aftherwards, Lynch, *et al.,* (2014) created the first national program for snake conservation in Colombia, in which it was stated that among the five threats previously identified, the major sources of snake mortality are habitat loss (50.000.000 dead snakes/year per municipality) and intentional snake killing by field workers and peasants (8.000.000 dead snakes/year per municipality).

Despite the efforts made by Lynch, *et al.,* (2014), their assessment have methodological gaps and shortcomings that hinder the suitable estimation and evaluation of the threats that contribute to the decline of snake populations in Colombia, particularly, with regard to intentional snake killing. For intance, the estimation and evaluation of snake killing ignores factors such as: 1) the inclusion of other taxa such as caecilias, amphisbaenids and limbless lizards that are easily confused with snakes; (2) the intensity and frequency of snake killing was based on occasional and non-structured interviews to peasants and field workers, which in turn caused bias on the snake killing rate estimation; (3) the space-time relations between the agricultural activities and snake activity that provokes encounters with snakes were not considered; and 4) the abiotic (e.g. seasonality) and biotic factors (e.g. availability of food and thermal resources, differential mobility between sexes or sizes, or resilience of populations to disturbance events) that might influence the human-snake conflict were not studied. Therefore, the methodological approach employed by these authors does not allow for testing the predictions derived from the "intentional snake killing by peasants and field workers represents a threat for snake conservation in Colombia” hypothesis.

With this in mind, and being aware that the success or failure of a conservation strategy depends on the proper prioritization of the threats, as well as the available resources and financial sacrifices that decision makers are willing to bear (Tilsdell and Nantha, 2011). The doctoral thesis " *Demographic analysis of intentional snake killing as a conservation threat: study case for a population of the species Ninia atrata*" aims to test the hypothesis that intentional snake killing by field workers represents a threat for snake conservation. This hypothesis generates several falsifiable predictions on the expected demographic responses toward this source of snake mortality.

For this purpose, this thesis is divided into four major chapters, written as scientific articles, which explore the life history traits, as well as the interaction between demographic processes and intentional snake killing by humans on a population of the snake *Ninia atrata*. The study was developed at an oil palm plantation of PALMASOL S.A. at municipality of San Martin, (Meta-Colombia) during 2014-2017, with an investment of 1189 hours of sampling effort. To test the expected demographic responses toward the intentional snake killing, a novel method of Integral Projection Model (IPM) was employed as a demographic approach.

The first chapter titled "*Life history traits*" makes a comprehensive description and analysis of the reproductive phenology (epigraph 6.1), feeding ecology (epigraph 6.2) and behavior (epigraph 6.3) of *Ninia atrata.* These life history traits are the raw materials to build the vital rates used the implementation of the IPM.

The second chapter titled "*Snakes in the palms: Snake-human conflict assessment at oil palm plantations (Meta-Colombia)*"characterizes the intentional snake killing pattern observed in an oil palm plantation, and illustrates how both abiotic and human factors affect the human-snake conflict. Also, this chapter provides the intentional snake killing rates used to generate the snake killing scenarios modeled in the IPM.

The third chapter titled "*Escaping from certain death: A demographic assessment of the intentional snake killing by humans*" describes the demographic approach and the methodologies to implement the IPM, and tests the demographic predictions under different snake killing scenarios. Finally, the fourth chapter summarizes the discoveries, discussions, conclusions, as well as the future insights from the development of this thesis.

This study seeks to improve our knowledge about links between the threats for snake conservation, snake´s demographic processes and their habitat peculiarities. This is accomplished, through an accurate revision of the determinant factors that affect human-snake conflict and its relation to intentional snake killing, to ameliorate the implementation of the national snake conservancy program in Colombia.

5. State of art and study context

5.1.1 Snakes studies in Colombia

Snakes are reptiles that exhibit amazing morphological adaptations, elegant forms and conspicuous behaviors that have captured the attention of researchers and unaware people that find them in the countryside (Fitch, 1999; Lillywhite & Seymour, 2011). But fear and antipathy toward snakes universal seem to be the main causes of snake aversion by many Colombians (Lynch, *et al.*, 2014), as well as the major sources of wrong impressions that have generated myths about these reptiles. For instance, serpents who bite with their tails, vipers who chase their victims for miles until they are exhausted so they can bite them, snakes that feed sucking the breasts of pregnant women and snakes that use their pestilential and penetrating yawn to stun and immobilize their victims to devour them slowly. These are some of the myths that enrich negatively the Colombian culture about snakes. Because of these astonishing myths, Colombians have a poor understanding about the diversity, biology and ecosystem services provided by more than 290 snake species that inhabit in the country.

Currently, Colombian researchers have serious obstacles to answer basic questions such as the ones asked by a child who discovers a snake in his backyard: “What does a snake eat? How old does a snake live? How many offspring can a snake have? Where does a snake live?” Thus, imagine trying to answer questions with greater relevance such as: “How does the expansion of the agricultural and mining frontier in the country affect snake populations?

These difficulties come from the historical poor development of snake studies in Colombia. Chronologically, the first study was made by Doctor Evaristo García Piedrahita (1845-1921) whom in 1896 published “Los ofidios Venenosos del Cauca”. This book presents a detailed study of the classification of venomous ophidians, including the diagnoses of the poisonous apparatus, its poisons effects, poisoning symptoms caused by snake bites, and empirical methods used against snake bites envenomation. García-Piedrahita begins the tradition of Doctors rather than biologists will developed snake studies in Colombia.

Some years later, Afranio do Amaral (1894-1982), one of the most prominent Brazilian scientists of the 20th century, dedicated several volumes to Colombian snakes, reporting new records and species which were summarized in the compendium named “Study of Neotropical Ophidians” (Amaral 1924-1931). At same time, the brother Lasallist Nicéforo María (1888-1980) made great contributions to knowledge to the incipient knowledge of the Colombian snakes when building the first snake list of the country (Nicéforo Maria, 1942).

On second half of twenty century, studies of the Colombian snakes went from being few to scarce, increasing the low representation in the scientific bibliography, as well as the general ignorance about these organisms. In this period, only three studies have relevance to Colombian ophidiofauna knowledge. First, “Las Serpientes de Colombia: Guía práctica para su clasificación y tratamiento del envenenamiento causado por sus mordeduras” by Doctor Rodrigo Ángel (1982) who follows the same medical line describes in the García-Piedrahita work´s but having interest in the venomous snakes that inhabit in Antioquia department. Second, “Ofidios de Colombia” by Pérez-Santos & Moreno (1988). And third, “Diversidad de los Reptiles en Colombia”. These last works did not evaluate the quality of the records used, which led to the underestimation of snake species richness for the country (240 and 219 snake species respectively versus 295 species currently reported (Uetz, et al., 2016), as well as to generate confusion about its distributions within the national territory. Particularly, Pérez-Santos & Moreno (1988) work were deeply criticized by Cadle (1992) who concluded that this work does not help in the compression of the snakes of the country, on the contrary, it generates noise, disinformation and confusion on the Colombian snakes (Lynch, et al., 2014).

A new century was need to impulse the snake research in the country. Since first decade on twenty one century, a growing number of publications have been improving the Colombian ophidiofauna knowledge. Subjects such as taxonomy, geographic distribution, Systematic and toxicology have covered by several researchers whom have tried to reduce the knowledge gaps of past (see Otero-Patiño, 2001, Shiel & Grant, 2001, Renjifo & Lundberg, 2003, Rueda & Rueda, 2004, Silva Haad, 2004, Ayerbe & López, 2005, Castro et al., 2005, Lynch, 2009, Passos *et al.,* 2009a, 2009b, 2009c, 2009d, Lynch, *et al.,* 2014; Angarita-Sierra, 2009, 2014, 2015; 2017, among others). Despite of this huge amount of contributions, issues such as ecology, fossil history, behavior, demography, ecophysiology, activity patterns, status, conservation and management remaining to be explored.

Particularly, in Colombia on 2007 the academy and environmental governmental entities realized the first attempt to build a conservation and management initiative which seeking to set up the basis of the national program of snake conservation. As results, Lynch (2012) made the first assessment of the threats for snake conservation, and Lynch et al (2014) erected the national program of snake conservation as policy paper. These documents state that primary sources of snake mortality are habitat loss (>50.000.000 dead snakes/year/region) and snakes killed by people (>8.000.000 dead snakes/year/region). However, despite the efforts in the evaluation of the threats made by these researchers, the presented estimates have gaps and methodological shortcomings that could hinder the effectiveness of this conservation strategy. Taking into account that makes environmental decisions without robust characterization of the threat that causes the snake population decline can lead to wasted resources, resulting in the conservation of fewer species than could have been achieved if the optimal set of actions had been taken (Yokomizo, et al., 2014), it is necessary to revisited the evaluation of the threats for snakes conservation in order to improve its future implementation.

5.1.2 Demographic studies of snakes

Population dynamics modeling has developed explosively for the last 40 years (Lebreton, 2006). This advance has been made possible by the huge efforts to understand vertebrate population dynamics (mainly birds) to resolve questions such as how size-specific harvesting does rate influence population dynamics and trait evolution? (Wallace, *et al.,* 2012), or how many populations must be preserved to avoid extinction for a specific time period? (Morris, *et al*., 1999).

There are at least four reasons to vertebrates be the major focus of the population dynamics modeling development: a wide diversity of life cycles (generation time ranges from a few weeks in small rodents to decades in whales or elephants); the fact that vertebrates can be counted, observed and marked relatively easily; the concerns on the impact of human activities on vertebrate populations (Eldredge, 1998; Thomas, *et al.,* 2004; Lebreton, 2006); and due to its charismatic nature, the general public has high empathy with them that helps to gather financial support to monitoring and conservation initiatives (Dobson, 2005).

However, snakes are vertebrate that have not the same popularity and empathy like MPMs esthetically pleasing species (particularly birds and mammals. Indeed, historically, laws on several countries have supported bounty systems for catch and kill snakes, organized hunts as cultural practice (e.g. Rattlesnake roundups), or kill snakes when they are consider dangerous species or a threat (Dood, 1987, Franke, 2000). Therefore, financial support devoted to snake conservation initiatives is very limited (Burghardt, et al., 2009).

Also, perception among researcher is that snakes have a secretive nature with elusive habits, cryptic behavior, and low densities, which make them difficult to study (Parker & Plummer, 1987; Dorcas & Willson, 2006; Guimarães, *et al*., 2014). Hence, the population dynamics framework has fewer studies that consider snakes as study organisms than other vertebrate taxa. Regardless, snakes have been proposed as model organisms, particularly, they have been the major aim of numerous studies in ecology and conservation biology (Bagshaw & Brisbin Jr, 1984; Bonnet, *et al*., 1999; Bronikowski & Arnold, 1999; Fitch, 1999; Shine & Bonnet, 2000; Almeida-Santos, *et al*., 2006; Dorcas & Willson, 2006; Miller, *et al.,* 2011; Guimarães, *et al*., 2014).

Most studies on snake population dynamics have been carried out with species at temperate latitudes (Fitch, 1978, 1999; Bagshaw & Brisbin Jr, 1984; Bronikowski & Arnold, 1999; Weatherhead, *et al*., 2002; King, *et al*., 2006; Hyslop, *et al*., 2009; Faust & Blomquist, 2011; Luiselli, *et al*., 2011; Hileman, *et al*., 2015). As consequence, a historical disparity occurs between the number of researches on temperate and tropical zones (Parker & Plummer, 1987). Hence, the snake population dynamics framework has been built from comprehensive information of many temperate snake species, but also with huge information gaps of tropical snake species.

This dearth of information is significant considering that richness is orders of magnitude higher in many tropical areas than in the temperate zones, and most lineages of snakes attain their greatest diversity in the tropics (Cadle, 1985, 1992; Cadle & Greene, 1993; Brown & Shine, 2002; Campbell & Lamar, 2004; Harvey, 2008; Wallach, *et al*., 2014). For example, in South America inhabit at least 794 snake species being the second continent with highest richness of world (Uetz, *et al.,* 1995). However, to date, only one species *Bothrops insularis* has population dynamics study (Guimarães, *et al*., 2014). Therefore, for a truly understanding of the population dynamics of snakes is necessary conducting numerous studies with species that inhabits in the tropics (Brown & Shine, 2002).

Traditionally, snake population information was anecdotal, collected as surplus information derivate from other research objectives, and frequently based on specimens collected from widely scattered localities (Seibert, 1950; Parker & Plummer, 1987). Towards the second half of the twentieth century appear the first results of long-term snake population studies (Brattstrom, 1953; Choate, 1963; Fukuda, 1969; Clark, 1970; 1974; Fitch, 1975; 1978; Parker, 1976; Feaver, 1977; Freedman & Catling, 1978) and in 1980s and 1990s were built up the classic snake population studies (Madsen, 1983; Brown & Parker, 1984; Plummer, 1985a; Seigel, 1986; Fitch 1999).

In general, all these contributions are based on top-down models which focused on highly aggregated state variables such as ecosystem function, population density, size population, sex ratio, age/size structure and mortality that affect density or number of species (Fahse, *et al.,* 1998). The main design criterion of top-down models is that they can be formulated with equations or classical deterministic approaches (Grimm & Railsback, 2004). Hence, their success in making snake ecology more predictive is limited because classical approaches are not testable as a rule; therefore, they do not directly contribute to the scientific cycle of hypotheses, predictions, and testing (Grimm, 1994).

Also, the prediction limitations of the classical models have been consequence of the a priori choosing of the level of aggregation instead of testing which elements of a real population should be considered in more detail (Fahse, *et al.,* 1998). In order to get a deeply understanding, as well as prediction capacity of the variation in the size and structure of snake populations, researches haven implemented several methodological approaches that can be grouped under name of Individual-based models (DeAngelis & Gross, 1992; Fahse, *et al.,* 1998).

In general, all this methods are bottom-up approaches that start at the bottom level, the individual level. This implies that individual´s properties, elements and performance are the main components that shape the features of the overall population. Therefore, a population increases or decreases depending on the rates at which individuals are born, mature, reproduce, and die (Easterling, *et al.*, 2000).

In this methodological approach, the major goal is to detect and analyze differences in life history traits among groups of individuals through time and space, which in sum, might induce changes in the fecundity and survival population rates, thus, in the population fitness (Lebreton , *et al.,* 2006). Most snake population dynamics studies developed have followed capture-recapture models (CRM) oriented to estimation of survival rates and birth rate using as a basic structure several survival models (Bronikowski & Arnold, 1999; Bonnet, *et al.,* 2002; Shine & Mason, 2004; Luiselli, *et al.,* 2011).

Likewise, the structured demographic models have been used to provide an accurate descriptions of snake population dynamics, by adding biological differences among individuals and the way that those differences affect individual´s fates in a given environment (Caswell & Fujiwara, 2004; Stanford & King, 2004; Alwtegg, *et al.,* 2005; Whiting, *et al.,* 2008; Miller, *et al.,* 2011; Hyslop, *et al.,* 2012; Bishop, *et al.,* 2016). Despite of life tables and matrix models have become extremely popular among ecologists, the implementation of these techniques to understand the snakes population dynamics have been poorly explored (Alwtegg, *et al.,* 2005; Hyslop, *et al.*, 2012). Even though toolbox of techniques for their analysis have been well-developed, the most common reasons that explain the scarcity of studies are: Firts, the difficulty to the accurate determination of individual age/stage when the snakes does not use dens, or have not aggregation behaviors (Fitch, 1999); and secondy, the misperception that their secretive natures make them difficult to study (Dorcas & Willson, 2006).

The matrix projection models are popular because they have relatively simple structure and provide useful information (e.g., growth rate, the stable age or stage distribution, reproductive value, and the sensitivities of population growth rate to changes in life history parameters), and can be parameterized directly from observational data on the fate and reproductive output of individuals (Caswell, 2001; Ellner & Rees, 2006).The matrix population model operates in discrete time projecting a population from t to $t_{+ 1,}$ regardless that the population has been characterized by a continuous state variable (e.g., mass, snout-vent length), individuals must be divided into a discrete set of classes. In some cases, the division may be natural (e.g., insects which can be grouped in instars), but often the division is artificial (Akçakaya, *et al.,* 1999; Easterling, *et al.,* 2000).

Because matrix population models are bottom-up approaches, the stage classification of the individuals is the keystone to construction, analysis, and interpretation of the population dynamics. However, the discrete set of classes that give to matrix population models its simplicity, handling and popularity, also gives its limitations and weaknesses. For instance, if the model has too few classes, biological realism is sacrificed, because highly dissimilar individuals are treated as if they were identical. (Easterling, *et al.,* 2000). On the other hand, If the model include too many classes can lead to parameter estimation problems, as each new class requires a new set of parameters to specify its mortality, fecundity, and state transition rates (Easterling, *et al.,* 2000; Caswell & Fujiwara, 2004). Likewise, the stage classification implies a temporal dimension in which development through a life stage takes time, and the amount of time often varies between individuals (De Valpine, *et al.,* 2014). These facts are important because the distributions of stage durations, due to individual variation in development, have a direct impact on population growth rate, sensitivities and elasticities as well as the able to comparisons both within and between species (Caswell, 1983; Ellner & Rees, 2006; Birt, *et al.*, 2009; De Valpine, *et al.,* 2014).

Easterling *et al.,* (2000) proposed the integral projection model (IPM) as novel alternative method that resolve the artificial discretization imposed by matrix population models (Caswell, 2001; Wallace, *et al.,* 2012; Merow, *et al.,* 2014). This model allow that the dynamics of continuous phenotypic character distributions can be tracked and linked with survival, development, inheritance and Fecundity (Coulson, 2010; Wallace, *et al.,* 2012) Also, generalized IPMs allow a mixture of both discrete and continuous characters to be modelled retaing the most useful properties of matrix projection models (Rees & Ellner, 2009).

On the other hand, only four character–demography functions (survival, development, inheritance and Fecundity) need to be characterised to construct an IPM (Ellner & Rees, 2006). These four functions describe the relationships between a character at time t and: (i) survival from time t_0 to time t_{+1}; (ii) development of the character among survivors from time t_0 to time t_{+1}; (iii) recruitment at time t_{+1}; and (iv) inheritance, which describes the relationship between offspring character values at time t_{+1} given parental characters at time t

(Smallegange & Colson, 2013). Therefore, IPMs protudes as new method that offer the potential to improve our understanding population dynamics throughout Individual-based model. Also, this method provide a powerful tool for quantifying how the vital rates of individuals govern such higher-level properties, partly because they rely on the flexibility and simplicity of regression models (Merow, et al., 2014).

Particularly, IPMs represent a good alternative to carries out studies of population dynamics in species with elusive habits, cryptic behavior, and low densities, like snakes, due to: First, the minimum data required for an IPM consists of two censuses of individual state and fate. Second, IPMs require many fewer parameters than matrix projection models when fitted to same data Third, because IPM are usually is parameterized by simple regressions (continues functions), regardless of the increase on size categories or individual-type within population assessed, the model does not suffered over-parameterization. Finally, IPMs are more suitable for estimating λ and elasticities from small data sets (<300individuals) than traditional matrix population models (Ramula, et al., 2009).

5.1.3 Literature cited

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6. CHAPTER 1: Life history traits

6.1 Great food is like great sex: exploring the reproductive ecology of the semifossorial snake *Ninia atrata*

6.1.1 Abstract

This study describes the reproductive ecology of a *Ninia atrata* population that inhabits in an oil palm plantation based on histological and field studies. Herein I assess whether environmental factors rather than intrinsic reproductive traits are the main drivers of the reproductive output. As results, prey abundance and food intake shown to be a crucial variables that contribute to reproductive output in *Ninia atrata*. Particularly, neonates showed high sensitivity to extreme climate changes being strongly related to slug and snail abundance variability and microhabitat quality. Reproductive cycles between sexes were noticeably different, being continuous cyclical in males while cyclical in females. Despite of this discrepancy, reproduction cycles at the population level in *Ninia atrata* is seasonal semisynchronous, mating is continuous throughout the year, and this is evident in small individuals, which show a high precocity in the species. Finally, reproductive output has a divergent response between sexes. In females, intrinsic reproductive traits are more critical than environmental variables. In males, environmental variables rather than intrinsic reproductive traits contribute more to reproductive output. Nevertheless, in both cases the relationship between body mass, prey abundance and food intake suggest that *Ninia atrata* employ an income breeding strategy in order to compensate reproduction costs and maximize fitness.

Key words: Continuous reproduction, spermatogenesis, oogenesis, clutch mass, reproductive effort, iteroparity.

6.1.2 Introduction

Since Fitch's (1970; 1982) early efforts to elucidate the reproductive cycles of tropical reptiles, studies of reproductive phenology of tropical snakes have increased in the last three decades as response to the historical disparity between the number of researches on temperate and tropical zones (Mathies, 2011). Particularly, in the South American tropics of Brazil and Argentina researchers have been leading and expanding the knowledge about the phenology and reproductive traits of almost ten elapids species, ten vipers species, nine boine and 26 colubrids species (Marques, 1996; Almeida-Santos, et al, 1998; Almeida-Santos, et al. 2006; Ávila, et al. 2010; Marques, et al. 2013, Almeida-Santos, et al. 1999; Valdujo, et al. 2002; Nogueira, et al. 2003; Janeiro-Cinquini, 2004; Hartmann, et al. 2004; Almeida-Santos & Salomao, 2002; Monteiro, et al. 2006; Marques, et al. 2013; Leãço, et al. 2014, Bretona & Chiaraviglio, 2003, Chiaraviglio, 2006, Pizzato & Marques, 2007, Rivas, et al., 2007, Miranda, et al., 2017, Marques, 1996; Vitt, 1996; Marques & Puorto, 1998; Hartmann, et al, 2002; Pizzatto & Marques, 2002, 2006; Balestrin & Di-Bernardo, 2005; Bizerra, et al. 2005; Pizzatto, 2005; Pizzatto, et al. 2005; Ávila, et al. 2006; López & Giraudo, 2008; Pizzatto, et al. 2008; Leite, et al. 2009; Marques, et al. 2009; Scartozzoni, et al. 2009; Alencar, et al. 2012; Gomes & Marques, 2012; Gaiarsa, et al. 2013; Braz, et al., 2014, da Costa-Prudente, et al. 2014).

All these contributions have built a new framework, in which the snake reproductive phenology take distances from the uniformly seasonal and highly synchronous patterns seen in species from temperate zones, towards aseasonal reproductive cycles with high variable synchrony among individuals of the same species (Pizzatto, et al. 2008; Mathies, 2011). However, the aseasonal reproduction is not the rule in the tropics; the broad variability in the reproductive ecology of the tropical snakes include multiple combinations of reproductive phenologies so that one can find many species with highly seasonal reproductive schedules (e.g. Naja spp, Bungarus spp, Calliophis spp) (Saint Girons & Pfeffer, 1972), as well as snake populations with intersexual divergence in their reproduction cycles (Pizzatto, et al., 2008).

Despite of these enormous efforts to understand the reproductive phenology of the snakes, fossorial and semifossorial tropical snakes have fewer studies than terrestrial or arboreal snakes (Braz, et al., 2014). This is due to fossorial and semifossorial snake's cryptic behavior, secretive microhabitats and lower encounter rate that make them an elusive research objective. Therefore, their natural history and ecology have been poorly understood, which limit our capability to assess their reproductive seasonality, the timescale of energy acquisition and expenditure on reproduction, ages or sizes of sexual maturation, as well as the environmental determinants that regulate their reproductive output (Brown & Shine, 2002, Balestrin & Di-Bernardo, 2005).

As part of an ongoing study of population dynamics, the reproductive phenology of the semifossorial snake *Ninia atrata* (Hallowell, 1845) was explored. *N. atrata* is the most widely distributed species of the genus in South America. It ranges from western Panama, Colombia, Ecuador, Venezuela and to Trinidad and Tobago (McCranie & Wilson 1995; Ingrasci 2011; Rivas et al. 2012; Angarita-Sierra 2009, 2014, 2015; Mesa-Joya 2015; Medina-Rangel 2015). Despite of its broad distribution and high abundance in disturbed or transformed habitats, its reproductive biology has been almost completely ignored (Angarita-Sierra 2015, Lynch, 2015). Currently, information available on the clutch size and birth-size in northern South America populations has been reported as anecdotal observations (Roze, 1966, Lancini, 1979, Natera-Mumaw, et al., 2015).

Therefore, the first goal in this study is to characterize the reproductive biology of *Ninia atrata*. Hence, histological and field studies are described. Also, the basic patterns of *Ninia atrata* reproductive biology such as spermatogenesis cycle, oogenesis cycle, annual reproductive cycle, minimum size at maturity for females and males, clutch size and egg features were documented. Second, considering that there is a range of widely environmental factors (e.g. food supply, climatic variability, microhabitat quality, among others) that are crucial determinants of reproductive output (Fitch, 1970, Shine & Madsen, 1997, Bizerra, et al., 2005); my secondary goal was to test whether environmental factors rather than intrinsic reproductive traits are the main drivers of reproductive output.

6.1.3 Methods

6.1.3.1Study area and data collection

Snakes were collected in the oil palm plantation (*Elaeis guineensis* Jacq 1897) of PALMASOL S.A. at vereda La Castañeda, municipality of San Martin, department of Meta -Colombia- (3°31´46, 6” N; 73°32´15, 3” W). The plantation is located on the foothills of the eastern slope of the Cordillera Oriental as well as on high savanna plateaus (Figure 1). This climatic zone is characterized by monomodal (rainy season from April to November, and dry season from December to March) climate with an annual rainfall of the 3,070 mm and high temperatures (> 26°C) year-round. Climatic variability was categorized as good and bad climatic years, where good years represent the sampling period from August 2014 to December 2015 without El Niño–Southern Oscillation (ENSO) effects, and bad years represent the sampling period from Jan 2016 to April 2017 under ENSO effects. Environmental temperature and relative humidity, as well as temperature and relative humidity of the microhabitats were monitored on a monthly basis using thermo-hygrometers model EBI 20-TH1 Ebro®.

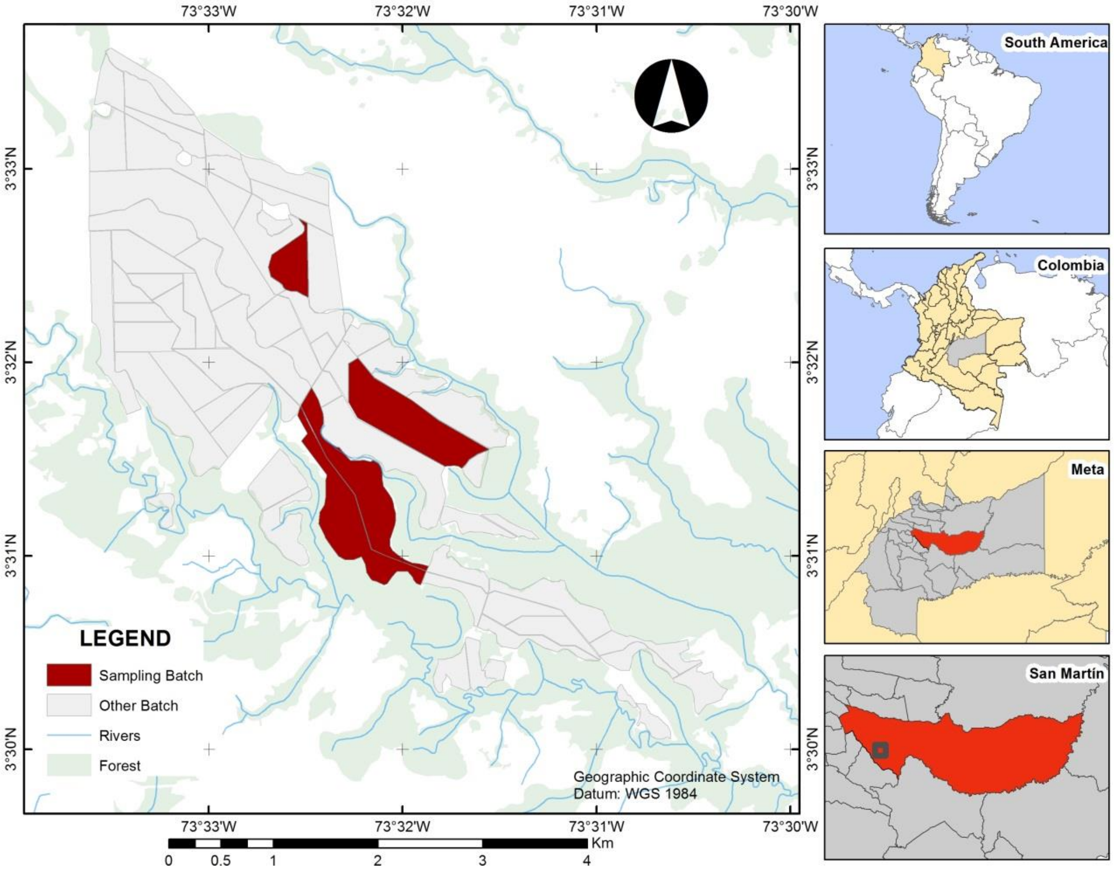

Figure 1. Study area. Oil palm plantation (*Elaeis guineensis* Jacq 1897) of PALMASOL S.A. Batches 8, 9, 13 and 15b in Red.

Sampling was conducted monthly from 7:30 to 17:30 during three sampling days, on period 2014-2017, in four production batches (Batch 8, 9 13 and 15b) that were separated at least one kilometer from each other. Batches 8, 9 and 15b were used as the extracting sampling area, and batch 13 was used for the mark-recapture experiments. All individuals of *N. atrata* were found by systematic removal of piles of palm leaves (microhabitat 1) as well as the epiphytic mattress from the base of the palms (microhabitat 2). The height of these microhabitats was measured (height in centimeters) before the removal. This measurement was employed as a surrogate estimator of the microhabitat quality. Immediately after removal of the microhabitats, the ground was raked up 5 to 15cm deep and the prey items sighted were recorded (snails, earthworms, slugs, and leeches). Once snakes were caught they were measured (snout–vent length= SVL; Tail length=

TL), weighed (Mass), and their health condition, sex, umbilicus scar, secondary sexual traits in males were registered. A sexual size dimorphism index (SSD) was calculated according to Gibbons and Lovich (1990).

Snakes captured in batch 13 were marked by branding ventral scales following the procedures describe by Dorcas & Willson (2006), and using an Aaron Medical Change-A-Tip cautery unit Bovie® (Winne, *et al.,* 2006). The presence of food and reproductive condition of the snakes was determined by palpation and through contrast light upon the snake body from dorsal to ventral surface. Sex of the marked snakes was determined by inserting a blunt probe through the anal orifice and following procedures described by Blanchard and Finster (1933). Afterwards, all the individuals branded were released at the same place in which they were sighted.

Gravid females and eggs found on the field were transported to the lab in individual terraria and provided with food and water *ad libitum.* Lab captivity environment was kept with the greatest similarity to the natural environment (Photoperiod regime: 12h light/12h darkness; Temperature: $\bar{x}$= 26.21°C ±0.61° and $\bar{x}$= 65.64 ±3.52%Hr). Eggs-laying were then collected, measured and inspected regularly throughout incubation ($\bar{x}$= 26.21°C ±0.61; $\bar{x}$= 65.64 ±3.52 Hr) and their temperatures were monitored using an infrared thermometer Model CGHM-H13. Newborn snakes were sexed, measured, individually marked and released with their mothers at the place in which the mother was captured.

Specimens collected from batches 8, 9 and 15b were sacrificed with an injection of lidocain 2% ($C_{14}H_{22}N_2O$) in the heart, fixed with 10% formalin and preserved in 70% ethanol. All the specimens were deposited in the reptile collection of the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia. Sex was determined by abdominal dissection and direct gonad observation. Besides, the reproductive tracts were fixed in 10% buffered formalin and used to make histological slides following the procedures described by Luna (1968) to determine the reproductive stage, as well as spermatogenesis and oogenesis cycles. Macroscopic and microscopic reproduction traits were registered following the procedures described by Krohmer, *et al.,* (2004), Balestrin & Di-Bernardo (2005) and Ramos-Pallares, *et al.,* (2015). The sperm abundance and time of occurrence of the spermatogenesis were based on counts (three times replicated) in cross sections of seminiferous tubules chosen at random using light microscope with 40x magnification (Fox, 1952). Male reproductive variables such as development degree of chin tubercules, size of hypertrophy of sexual segment of the male kidney (SSK), testicular volume, and width of distal end of deferent duct were assessed. Mature males were considered as the smallest (SVL) male having spermatozoa in the testicles. In females, reproductive variables such as uterine scars, oviductal width, number and diameter of previtellogenic and vitellogenic follicles, and oviductal eggs were evaluated. Also, relative fecundity (RF) and relative clutch mass (RCM) were calculated following Iverson (1987) and Seigel and Fitch (1984) respectively. Female reproductive condition were classified as previtellogenic (only translucent tiny follicles), vitellogenic (yellowish yolky follicles), ovigerous (with oviductal eggs) and vitellogenic and ovigerous (with vitellogenic follicles and oviductal eggs simultaneously). Mature female were considered as smallest female with vitellogenic follicles or oviductal eggs. Also, all previtellogenic and vitellogenic follicles were examined through cross sections cuts to validate its development stage. Clutch size was considered as the number of oviductal eggs in each female, or the number the eggs oviposited by each female. Finally, oviducts and Infundibulum were inspected by looking for sperm as surrogate estimator of mating season.

6.1.3.2 Statistical analysis

Differences in the sex ratio among mature males, and mature females at each month were assessed using a G-test and Chi-square (χ^2) test. Size of sexual maturity between sexes was evaluated using *t*-test assessing assumptions of normality and homoscedasticity employing Kolmogorov-Smirnov test and Levene test, respectively (Guisande-Gonzáles, et al., 2014). Monthly intersexual variations (synchrony) in the female and male reproductive stages, as well as its time variation (seasonality) were evaluated using a χ^2 test and G-test. Likewise, one way ANOVA was employed to compare the oviduct distal width between female reproductive stages.

To test whether environmental factors rather than intrinsic reproductive traits are the main drivers of reproductive output, multiple regression analyses were carried out. Therefore, the relationships between female reproductive output and environmental as well as intrinsic reproductive traits were assessed as follow: First, females reproductive traits such as: SVL (Var 1), body mass (Var 2), primary follicles number (Var 3), secondary follicles number (Var 4), fat body area (Var 5), and stomach bolus volume (Var 6) were considered. Likewise, environmental factors such as temperature and relative humidity of the environment (Var 7), temperature and relative humidity microhabitat 1 (Var 8), temperature and relative humidity microhabitat 2 (Var Z), and height of piles of palm leaves (Var 9) were employed. Particularly, variables Var 7, Var 8 and Var Z are the ratio between temperature and relative humidity of the respective microhabitat. Thus, Var 7, Var 8 and Var Z are quotients employed to perform the statistical analysis. Stomach bolus and fat body were measured through digital picture using Imagen–J software seeking to reduce to the maximum any error measurement to obtain repeatable measurements. Hence, stomach bolus volume was estimated employing Equation 1 .Similarly, fat body areas were calculated as the sum of the all polygons resultant of the fat body attached to digestive and reproductive tract of each individual.

$$V = \frac{3}{4}\,\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right)$$

Equation 1. Ellipsoid formula to calculate testes and stomach bolus volume. Where V= Testes volume estimated or stomach bolus; *w*= width and *l*= length.

Second, all variables assessed and clutch size observed were square root or natural logarithm transformed using Tukey's staircase transformation method described by Erikson and Nosanchuk (1977). Third, assumptions of normality, autocorrelation, and homoscedasticity were evaluated using Kolmogorov–Smirnov's test, Durbin–Watson test and Breusch–Pagan test, respectively. Fourth, multicollinearity between the variables previously named was tested using statistical technique of variance inflation factor (VIF) with a threshold of 10. Fifth, to select the "best" regression model based on the variables evaluated the Akaike Information Criterion was employed (AIC) (Akaike, 1973).

Finally, to estimate the contribution of all the independent variables to the regression model a hierarchical partitioning method was used (Chevan & Sutherland, 1991). All statistical analyses were done using the software Rwizard 2.3 (Guisande-Gonzáles, *et al.,* 2014) and the following *R* packages StatR (Guisande-Gonzáles, *et al.,* 2014), hier.part (Walsh & MacNally, 2015), nortest (Gross, 2015), lmtest (Hothron, *et al.,* 2017), and usdm (Naimi, 2015).

In a similar way to the exploration of the relationships between female reproductive traits and environmental variables, a multiple regression analysis was carried out to analyze the drivers of sperm production in males and neonate abundance. Therefore, the same tests of multicollinearity, normality, autocorrelation, and homoscedasticity, as well as same statistical techniques to select "best" regression were employed. Hence, the following variables were considered: SVL (Var 1), body mass (Var 2), stomach bolus volume (Var 6), testicular volume (Var 10), SSK width (Var 11), and width of distal end of deferent duct (Var 12). Particularly, to evaluate the neonate abundance, the regression models only considered environmental determinants as well as prey abundance (e.g. snails, slugs, leeches, and earthworm).

6.1.4 Results

A total 425 specimens of *Ninia atrata* (males=209, females=216) were caught during 2014-2017, reporting a sexual dimorphism index (SD) of 0.16. Also, the variation observed on sex ratio does not have significant differences between months (χ^2= 15.897, P= 0.145, n= 421) or climate season (χ^2 = 2.3091, P= 0.1286, n= 421). In contrast, significant differences in the snake abundance between good and bad climate years were found (χ^2 = 176.15, P< 0.0001, n= 421)

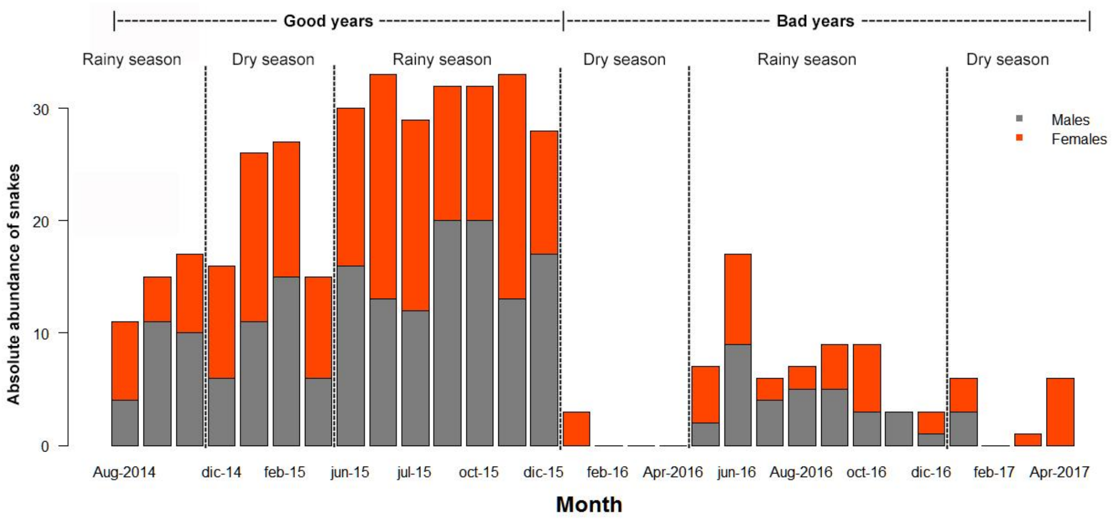

Figure 2. Abundance and population sex ratio of *Ninia atrata* through sampling period (2014-2017)

6.1.4.1Female reproductive cycle and activity

According with the macroscopic reproductive traits observed in 73 *Ninia atrata* females, the smallest female with vitellogenic follicles, indicating sexual maturity, was 270 mm SVL. All females' lager than 270 mm SVL (48%, n=73) seemed to be in some stage of reproduction (Table 1)

Reproductive stages variation in females was not significant between months or climates years (χ^2_{months}= 27.374, *P*= 0.44, n= 73; $\chi^2_{\text{climate years}}$= 3.0528, *P*= 0.38, n= 73). In contrast, oviduct width exhibited significant differences between reproductive stages (ANOVA F= 13.7, *P*< 0.0001, n= 73) distinguishing clearly the oviduct width on previtellogenic stage from the remaining stages. However, differences between ovigerous, vitollogenic, and vitollogenic plus ovigerous were not significant. Therefore, an oviduct width larger than 6.14 ±3.85mm indicates sexual maturity. Nonetheless, a high overlapping degree of the oviduct width between female reproductive stages was observed, suggesting that this macroscopic character is not an accurate predictor of sexual maturity (Figure 2).

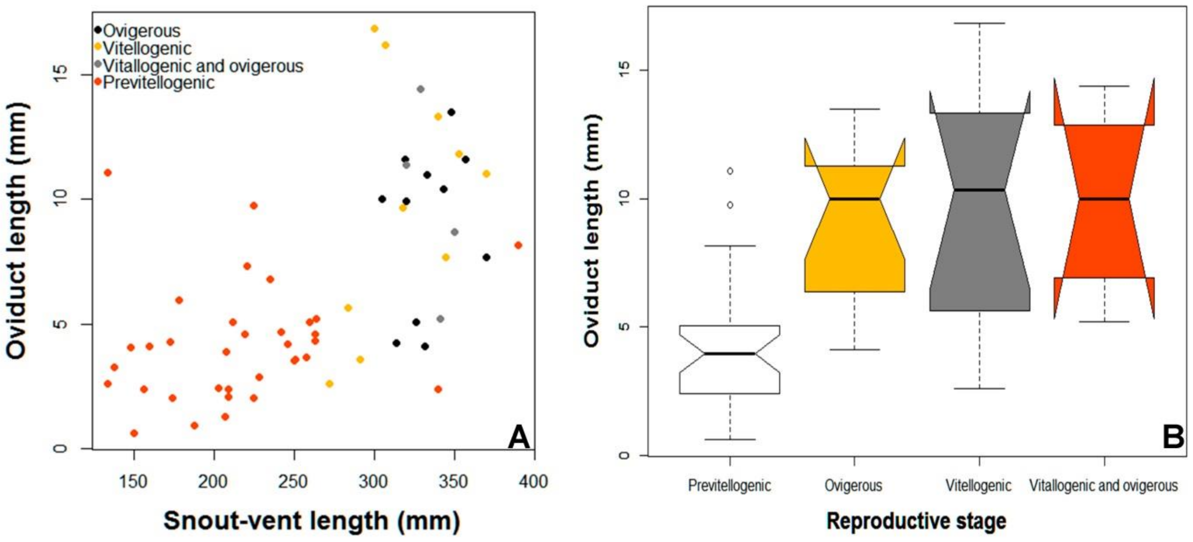

Figure 3 Variation on oviduct width. A) scatterplot depicting the relation the snake size (SVL) and the distended degree of the oviduct (mm). B) ANOVA analysis showing oviduct length differences between female reproductive stages.

As expected, the presence of uterine scars was significantly associated to reproduction stages (χ^2= 44.324, *P*<0.001, n= 69), where its occurrence is significant in ovigerous and vitollogenic stages, while at same time, it is significant absent in previtellogenic stage. However, uterine scars were observed in 15% (n=5) of the neonates or juvenile females (previtellogenic stage). Likewise, 40% (n= 43) of previtellogenic females over 225mm SVL presented oviductal sperm, of which the ones that have sperm into infundibulum were statistically significant (χ^2 = 23.38, *P*< 0.001, n= 43). This suggests that small females are willing or were forced by males to mate.

Besides, sperm inside infundibulum and oviduct was almost present throughout the year (except on December), indicating that mating is continuous. Even though the sperm was observed at non-reproductive states, mating depends on the female's reproductive stage (χ^2 = 20.14, *P*< 0.001, n= 73), particularly, previtellogenic females exhibited significant absence of sperm in the oviduct with respect to the remaining reproductive stages.

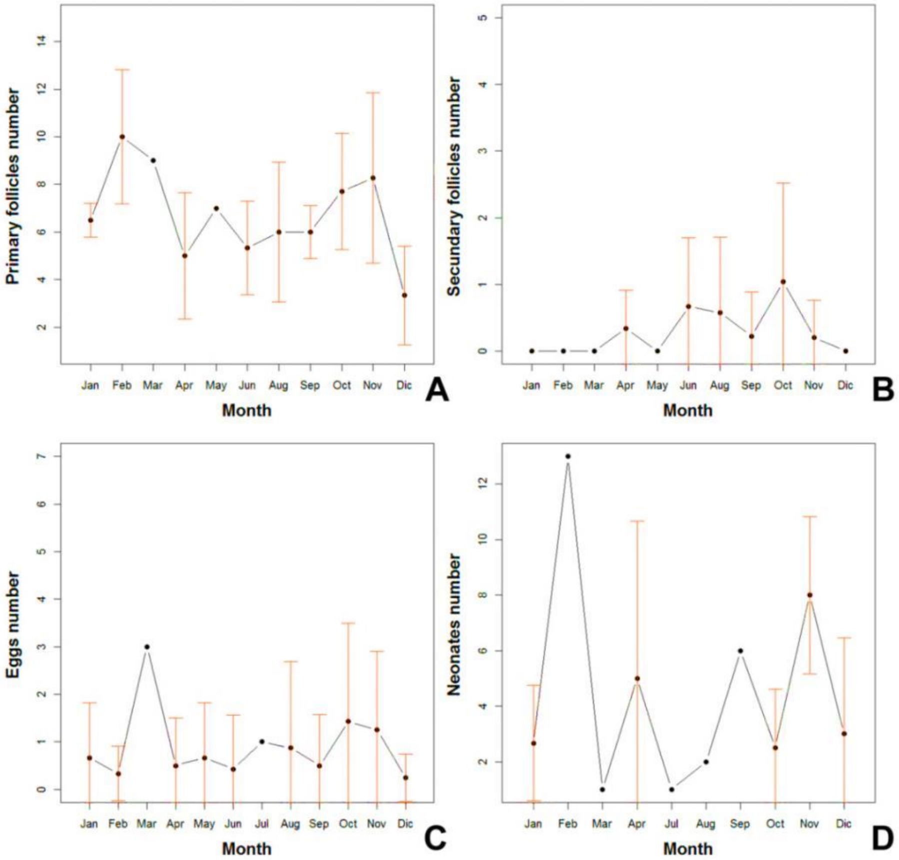

Figure 4. Monthly variability of female reproductive traits and neonates. Black dots represent mean value, orange bars represent standard deviation. A) Absolut values of primary follicles observed. B) Absolut values of secondary follicles observed. C) Absolut values of eggs found during the sampling period and observed on reproductive tracts dissected. D) Absolut values of neonates observed during sampling period.

In 78 adult females examined, primary follicles were present throughout year, however, on mid-June most of the follicles begin to enlarge, reaching its larger size between November-January until the beginning of the dry season (Figure 4A). Likewise, greatest abundance of primary follicles was observed between January-March and September-November. Consequently, secondary follicles were only observed from April to November (rainy season) in which its abundance and size increases gradually, reaching its greatest size during the October-November period (Figure 4B).

Table 1. *Ninia atrata* female's reproductive features.

Female reproductive stage	SVL (mm)	Mass (g)	Oviduct length (mm)	Sperm in the oviduct	Uterine scars	Number of primary follicles	Number of secondary follicles	Number of eggs
Previtellogenic	x̄=205.05 (120—246) N=38	x̄=4.94 (1.08—9.42) N=34	x̄=4.00 (0.91—9.75) N=38	Presence (40%) Absence (60%) N=43	Presence (15%) Absence (85%) N=38	x̄=5.71 (1—10) N=38	absent	absent
Vitollogenic	x̄=313.57 (270—353) N=14	x̄=12.01 (8.33—17.09) N=14	x̄=9.19 (2.59—16.85) N=14	Presence (87.5%) Absence (12.5%) N=16	Presence (20%) Absence (80%) N=10	x̄=7.21 (3—10) N=14	x̄=2.36 (1-5) N=10	absent
Ovigerous	x̄=335.08 (278—370) N=12	x̄=15.88 (13.33—19.8) N=11	x̄=9.06 (4.10—13.49) N=12	Presence (83.3%) Absence (16.7%) N=12	Presence (100%) N=12	x̄=8.66 (5—13) N=12	absent	x̄=3.25 (2—4) N=12
Vitollogenic and ovigerous	x̄=315.68 (320—370) N=5	x̄=15.02 (12.35—19.1) N=5	x̄=10.13 (5.19—14.4) N=5	Presence (100%) N=7	Presence (100%) N=5	x̄=10 (7—14) N=5	x̄=1.8 (1—3) N=5	x̄=2.8 (2—4) N=5

On the other hand, eggs were observed throughout most part of the year, having greatest abundance between September-December (Figure 4C). Based on the incubation of three clutches oviposited by three gravid females the birth-time estimated was 108 ±1.41 days per egg. Clutch sizes range from one to four eggs (x̄= 2.44 ±1.02, N= 34). In addition, a total of five vitollogenic and ovigerous females were recorded during September-November period, indicating that females can produce more than one clutch of eggs in a reproductive season.

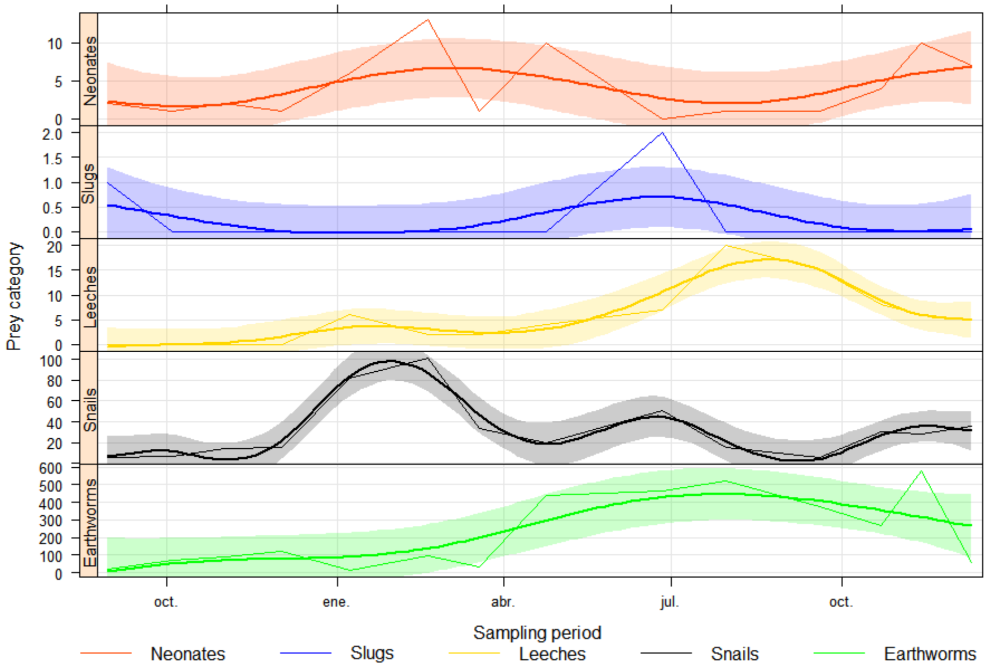

Figure 5.Temporal prey abundance variation and neonates of *Ninia atrata* during climate years without ENSO effects (2014-2015). Scale of the Y axis represents the absolute abundance values. Shaded area represents 95% confidence intervals. Zigzag lines represent the abundance values at each sampling period

In the same way of eggs, neonates were observed throughout most part of the year (except on July), having three abundance peaks during the recruitment season. The greatest recruitment peak occurs on mid-dry season (January-February). A second moderately recruitment peak was observed on September, and finally, a third pronounced recruitment peak took place at the end of the rainy season (November). Besides, they experience their greatest dearth on mid-rainy season (June-July) (Figure 4D). Based on the birth of eight neonates the birth-size was estimated as 114.63 ±10.69 mm SVL and 1.91 ±0.74g of body mass.

Likewise, relative clutch mass (RCM) and relative fecundity (RF) observed were highly variable and ranged from 4.32% to 8.54% ($\bar{x}$=7.21 ±1.14%, n= 16), and from 2.72% to 12.74% ($\bar{x}$=7.28 ±3.01%, n= 34) respectively.

On the other hand, between good and bad climate years a remarkable decrease of neonates was observed. On years with ENSO effects the number of neonates detected decline fourteen times passing from 57 records during good years to four records during bad years (χ^2 = 10.557, P= 0.001). Despite of this, during years without ENSO effects a clearly synchronization between recruitment peaks and prey abundance were observed. Increments in snails and slugs abundance coincide with rise of neonate abundance at the same time period (Figure 5). This relationship was confirmed by multiple regression analysis in which neonate abundance was strongly related with slug and snail abundances rather than remaining preys (Figure 6). The “best model” comprised by slug and snail abundances explains the 46.45% of the neonate abundance variability observed (R^2= 0.4645, P= 0.032). Nonetheless, when the environmental variables are included in the analysis these provide a better model that explain the 64.78% of the neonate abundance variability observed (R^2= 0.6478, P= 0.0032), being temperature and relative humidity of the environment, and height of piles of palm leaves the variables that exhibited the main relative importance and compose the “best model” (Table 2).

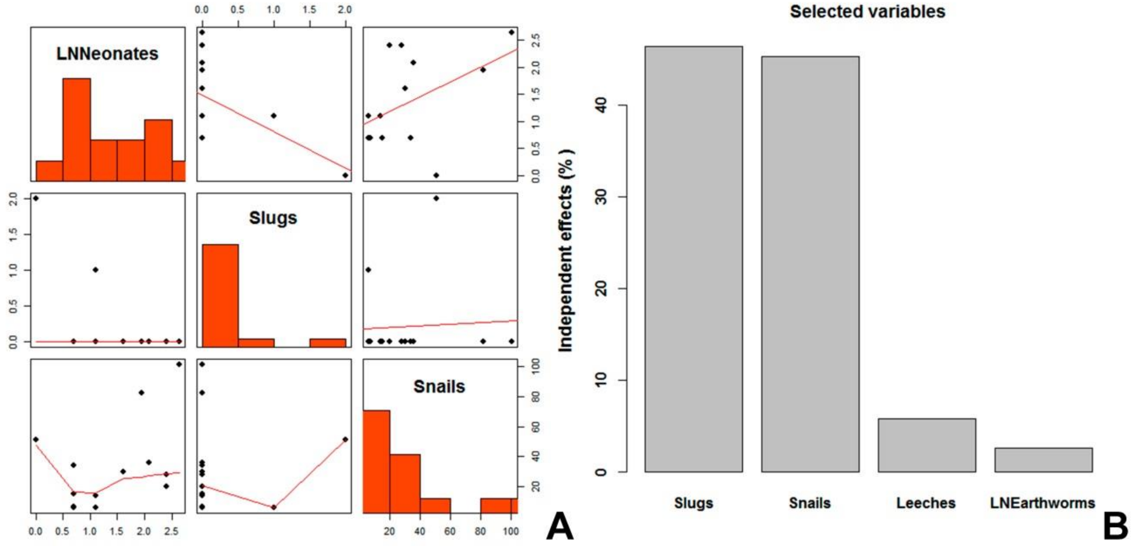

Figure 6. Multiple regression models that relate neonate's abundance with prey's abundance. A) Matrix plots depicting linear regressions between Neonate abundance and preys abundance. B) Relative contributions of the variables that assessed. LNNeonates= Logarithm transformed neonate abundance. LNEarthworms= Logarithm transformed earthworm abundance.

6.1.4.2Male reproductive activity

Ninia atrata males exhibited a striking early sexual activity. The smallest male with sperm in the testicles, indicating sexual maturity, was 145 mm SVL, and the larger male without sperm in the testicles was 212 mm SVL. These males represent extreme body size limits to sexual maturity. However, the 98.60% (n=71) of males larger than 187 mm SVL have sperm in the testicles and in the deferent duct. Also, the smallest male with metamorphosing spermatocyte was 137 mm SVL.

On the other hand, macroscopic examination of the gonads of *Ninia atrata* males reveals that the testicles show noticeably size variation throughout the year. Testicular size gradually changes, decreasing from February to August, and increasing from August to November reaching its maximum volumes on April (beginning of the rainy season) and October-November period (end of the rainy season), being 136.4% greater than the minimum testicular volume observed on August (Mid-rainy season) (Figure 7A). Despite the fact that there were not available samples of mature males on December, January and March, the data suggest that the testicular volume declines when the dry season starts and it increases during mid-dry season.

Likewise, macroscopic sexual features such as SSK and distal end of the deferent duct have a similar monthly variability pattern observed in testicles volume (Figure 7C-D). Indeed, the monthly variability of these traits were closely related to the testes size observed (R^2_{SSK}=0.68, P<0.0001, *n*=69; $R^2_{deferent\ duct}$=0.45, P<0.0001, *n*=69). In contrast, the sperm production does not show correlation with the monthly variability observed in the macroscopic male sexual features (R^2_{SSK}=0.031, P= 0.15, *n*=69; $R^2_{Testes\ volume}$=0.028, P= 0.18, *n*=69; $R^2_{deferent\ duct}$ =0.033, P= 0.14, *n*=69), indicating that testicles volume, SSK hypertrophy, and deferent duct width does not reflect concordantly the spermatogenic activity. Sperm production was present for the most part of year, including dry and rainy season, increasing gradually from April to November and reaching its maximum abundance on July-August (mid-rainy season) without significant drops once sperm production has begun (Figure 7).

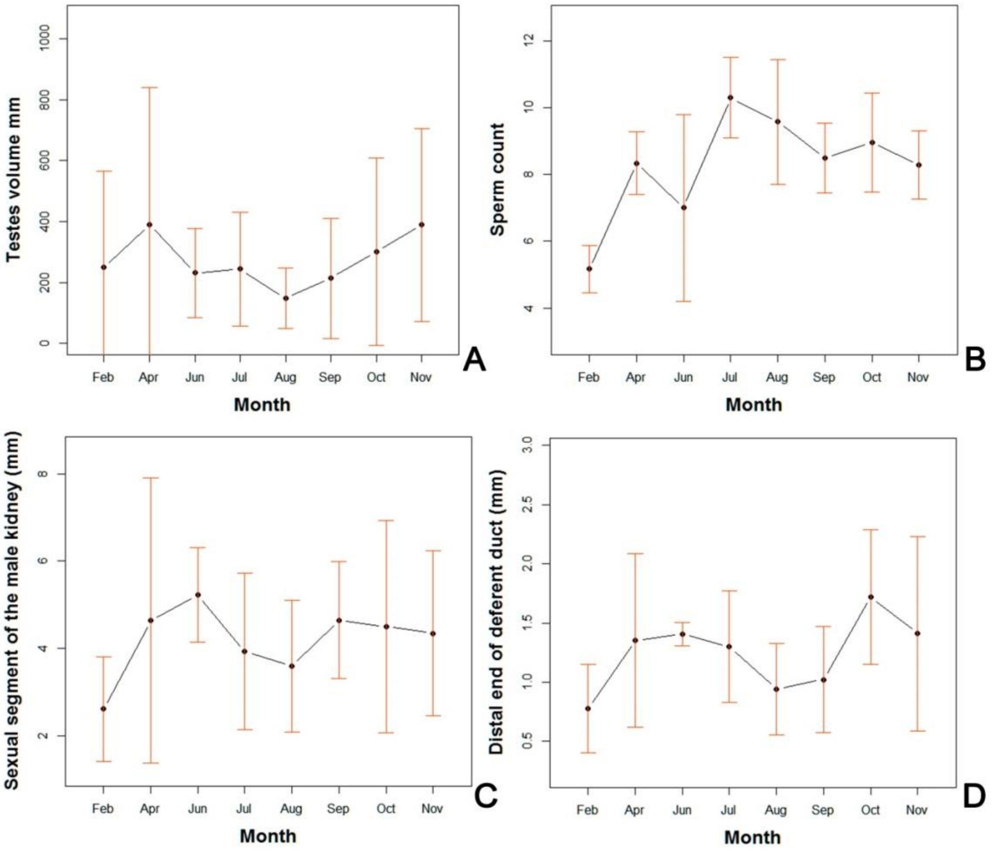

Figure 7. Monthly variability of male reproductive traits. Black dots represent mean value, orange bars represent standard deviation. A) Absolut values of testes volume observed. B) Average values of sperm count observed per individual. C) Width of sexual segment of the male kidney. D) Width of distal end of deferent duct.

On the other hand, significant differences in male sizes that present faint or prominent chin tubercles were found (ANOVA= 37.28, P<0.0001, *n*= 66). The faint condition was associated to males with SVL ranges between 135—241mm (x̄=168.16; n=12). However, two larger males (SVL= 276 and 280) maintained this condition even though they overcome the minimum size of sexual maturity observed. In contrast, the prominent condition was associated with males in which theirs SVL ranges between 183—354mm which agrees with 98.60% (n=71) of males that have sperm in the testicles and in the deferent duct. Similarly, there were three males with small sizes (SVL= 146, 154 and 175) who maintained this condition. Nevertheless, the SVL ranges show a high overlapping degree (46.53%) between chin tubercles conditions indicating that this secondary sexual character is not an accurate predictor of the male reproductive stages

6.1.4.3Reproduction cycles and mating

Notable differences in the reproductive cycles of *Ninia atrata* individuals between sexes were found. First, males showed a continuous cyclical pattern in which spermatogenesis, gonads and SSK exhibited activity throughout the year, having a reduced activity during dry or mid-rainy season, but never displayed a total regression or being quiescent. On the contrary, females showed cyclical pattern in which oogenesis, gonads or accessory organs become inactive or absents during dry season. Second, size of sexual maturity between sexes exhibited significant differences (t = 9.5443, P< 0.0001, n= 277) in which males attained sexual maturity at 56% of mean adult SVL and female at 86%. Finally, the higher values of sperm and vitellogenic follicles production are not synchronized. For instance, the maximum sperm abundance was presented in July-August period (mid-rainy season) while maximum vitallogenic follicles abundance was recorded during the October-November period (end of the rainy season).

Despite of the divergence on individual reproductive cycles between sexes, the sperm production and follicles maturation pattern observed indicate that the reproduction cycle at the population level in *Ninia atrata* is seasonal. Both sexes present a synchronized increment in their sexual activity through the rainy season, keeping their highest abundance from June to November. Even though no mating behavior observed among individuals of *Ninia atrata*, the high frequencies of oviductal sperm, as well as the sperm production and follicle maturation processes observed suggest two main pulses of mating, the first, during beginning of rainy season (April), and the second at the end of rainy season (October-November). However, evidence of mating was present throughout the all year including dry season (Figure 8).

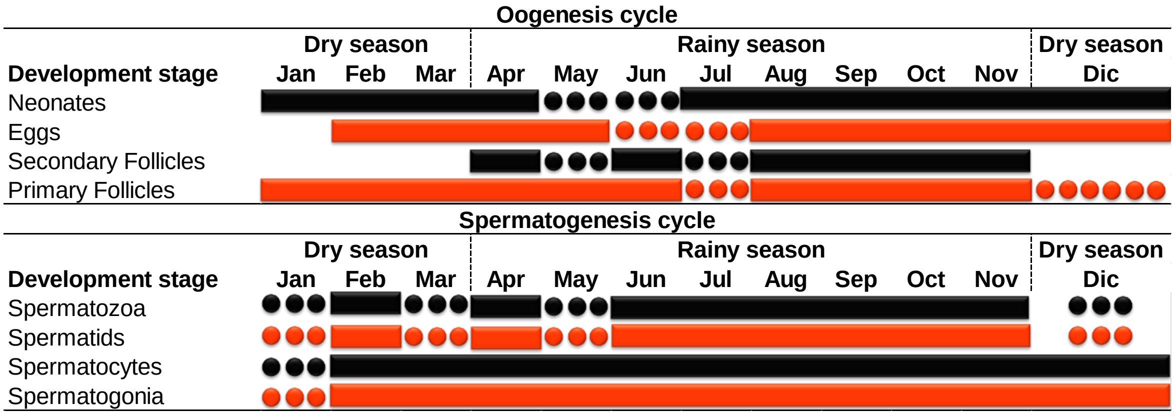

Figure 8. Oogenesis and spermatogenesis cycles in Ninia atrata. Females= 73, Males= 85. Boxes= observed, dotted line= inferred

6.1.4.4 Environmental variables versus intrinsic reproductive traits

Environmental variables and intrinsic reproductive traits showed a differential importance in the reproductive output between sexes. In female case, the multiple regression analysis indicated that clutch size was strongly related with almost all the reproductive traits evaluated (Table 2). However, between these variables the “best model” was comprised by the number of primary and secondary follicles, as well as body mass which explains the 70.63% of the clutch size variability observed (R^2= 0.7063, *P*< 0.0001). Given the importance of secondary follicles in the clutch size, a second multiple regression analysis was carried out exploring the relationship between secondary follicles, maternal traits and environmental variables (Figure 9). As a result, secondary follicles variability observed was highly related with stomach bolus volume, fat bodies area, and body mass. These variables compose the “best model” which explains the 44% of the secondary follicles variability observed (R^2= 0.437, *P*= 0.003). Similarly, female SVL rather than all other remaining variables assessed was significantly related with eggs mass (F= 7.646, *P*= 0.014, n=17), indicating that larger females produce heavier eggs.

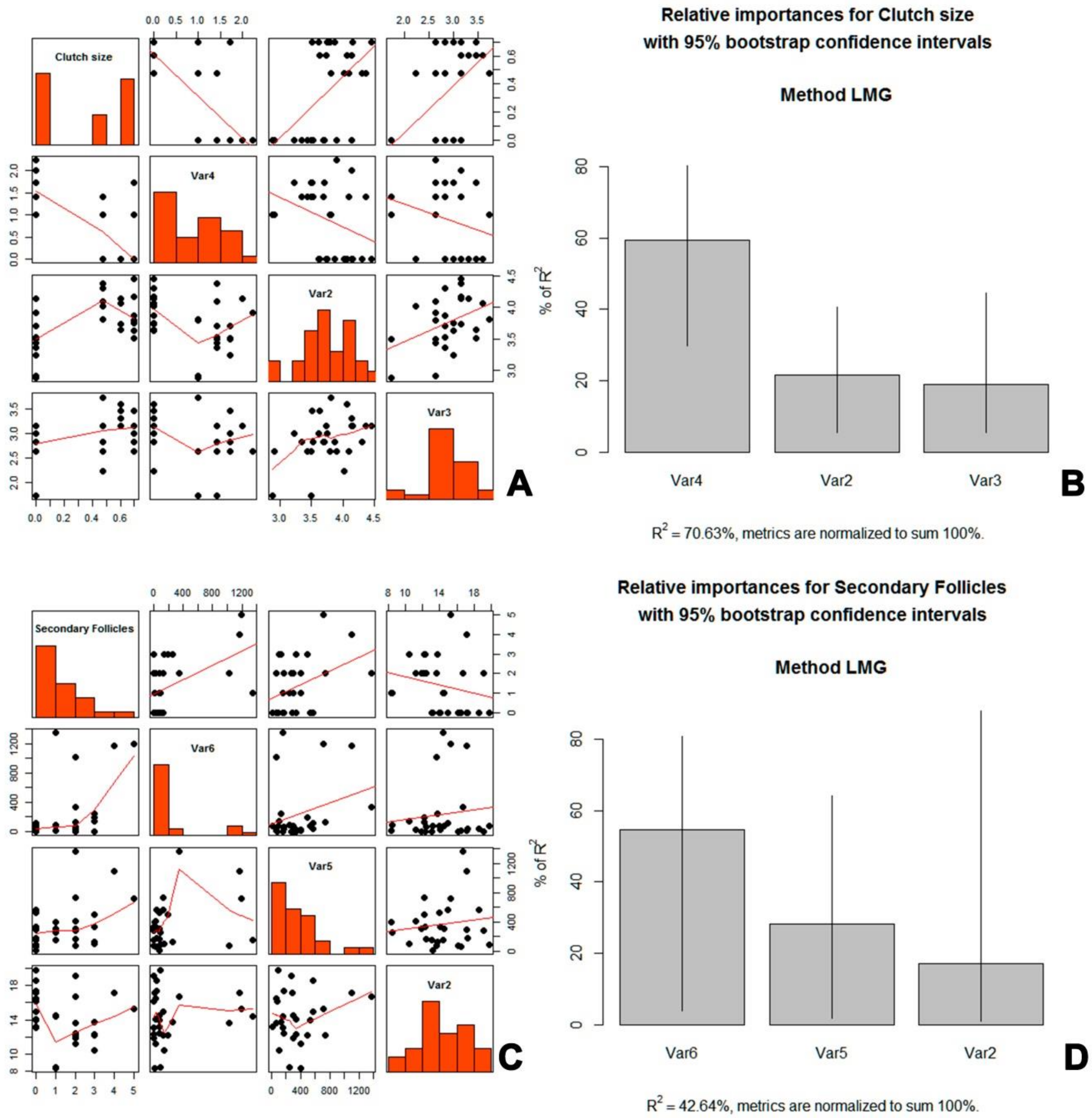

Figure 9. Multiple regression models that relates clutch size and secondary follicles with environmental variables and intrinsic reproductive traits. A and C) Matrix plots depicting linear regressions between clutch size and secondary follicles with variables assessed, respectively. B and D) Relative contributions of the variables that compose the "best regression model" for clutch size and secondary follicles, respectively. Var1= Snout-vent length, Var2= body mass, Var3= primary follicles number, Var4= secondary follicles number, Var5= fat bodies area, and Var6= stomach bolus volume.

In the case of males, the multiple regression analysis reveals that environmental variables and body size rather than intrinsic reproductive traits were the drivers of sperm production. The "best" model that explain the 24.12% of the sperm production observed is composed by body size, height of piles of palm leaves, stomach bolus volume, and temperature and relative humidity of the environment

(Table 2), being body size and height of piles of palm leaves the variables that exhibited the main relative importance between sperm production and the variables assessed. This result agrees with the discordance observed between sperm production and the monthly variation on size of the testicles and SSK width.

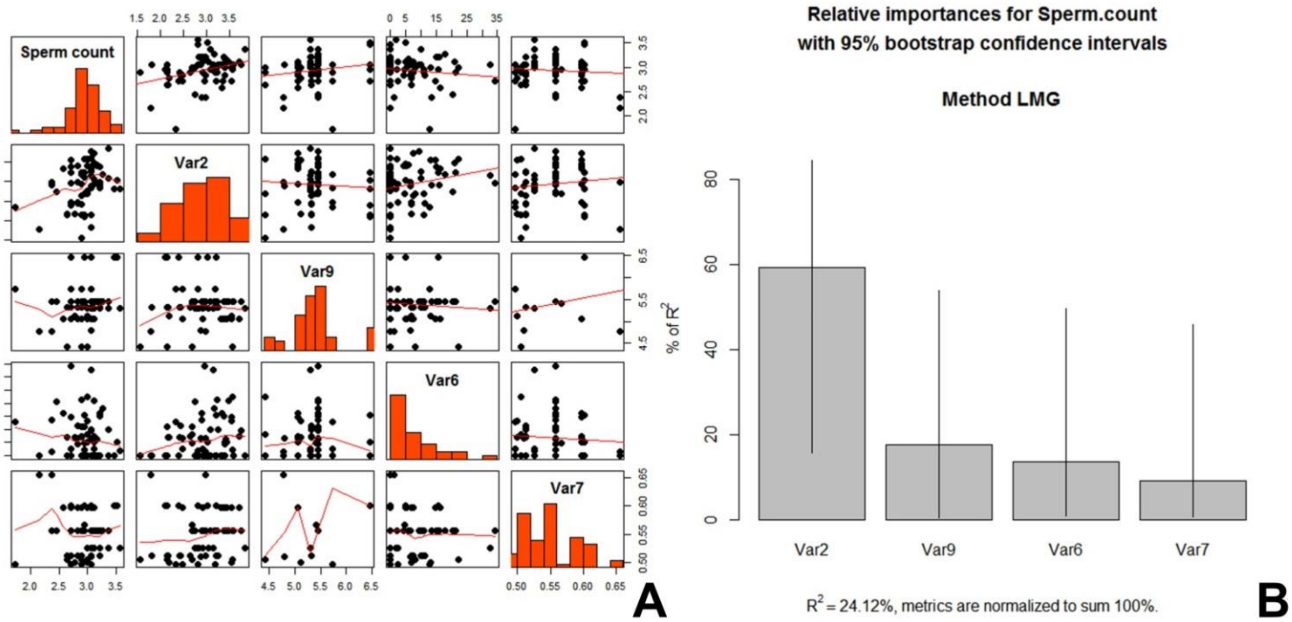

Figure 10. Multiple regression models that relates sperm production with environmental variables and intrinsic reproductive traits. A) Matrix plots depicting linear regression models between sperm count with variables assessed. B) Relative contributions of the variables that compose the "best regression model" for sperm count. Var2= body mass, Var6= stomach bolus volume, Var7= temperature and relative humidity of the environment, and Var9= height of piles of palm leaves.

Table 2. Multiple regression analysis models. Akaike Information Criterion (AIC) employed to select the "best model" used to test whether environmental factors rather than intrinsic reproductive traits are the main drivers of reproductive output. Var1= Snout-vent length, Var2= body mass, Var3= primary follicles number, Var4= secondary follicles number, Var5= fat bodies area, and Var6= stomach bolus volume, Var7= temperature and relative humidity of the environment, Var8= temperature and relative humidity of the microhabitat 1, VarZ=temperature and relative humidity of the microhabitat 2, Var9= height of piles of palm leaves, Var10= testicular volume, Var11= Width of the sexual segment of the kidney, and Var12= distal width of the deferent duct. Nor.test= Kolmogorov–Smirnov's test for normality, Hom.test= Breusch–Pagan test for homoscedasticity, and Aut.test= Durbin–Watson test for autocorrelation.

Model	AIC	dAIC	df	Nor.test P-value	Hom.test P-value	Aut.test P-value
Clutch size versus female reproductive traits and environmental variables						
Clutch size~Var2+Var3+Var4	-92.25	0.0	1	0.09	0.40	0.82
Clutch size~Var2+Var3+Var4+Var5	-90.94	-1.31	1			
Clutch size~Var1+Var2+Var3+Var4+Var5	-89.17	-3.08	1			
Clutch size~Var1+Var2+Var3+Var4+Var5+Var9	-87.22	-5.03	1			
Clutch size~Var1+Var2+Var3+Var4+Var5+Var6+Var9	-85.23	-7.02	1			
Clutch size~Var1+Var2+Var3+Var4+Var5+Var6+Var7+Var9+VarZ	-83.24	-9.01	1			
Secondary follicles versus female reproductive traits and environmental variables						
Secondary follicles~Var2+Var5+Var6	-22.82	0.0	1	0.80	0.49	0.65
Secondary follicles~Var2+Var5+Var6+Var8	-22.68	-0.14	1			
Secondary follicles~Var2+Var3+Var5+Var6+Var8	-22.03	-0.79	1			
Secondary follicles~Var1+Var2+Var3+Var5+Var6+Var8+VarZ	-18.41	-4.41	1			
Secondary follicles~Var1+Var2+Var3+Var5+Var6+Var8+Var9+VarZ	16.42	-6.40				
Sperm count versus male reproductive traits and environmental variables						
Sperm count~Var2+Var6+Var7+ Var9	-167.80	0.0	1	0.10	0.34	0.23
Sperm count~Var2+Var6+Var7+ Var9+VarZ	-167.51	-0.29	1			
Sperm count~Var2+Var6+Var7+ Var9+Var11+VarZ	-165.74	-2.06	1			
Sperm count~Var2+Var6+Var7+ Var9+Var10+Var11+VarZ	-163.98	-3.82	1			
Sperm count~Var1+Var2+Var6+Var7+ Var9+Var10+Var11+Var12+VarZ	-162.00	-5.80	1			
Neonates versus prey abundances						
Neonates~Slugs+Snails	-9.06	0.0	1	0.34	0.50	0.46
Neonates~Slugs+Snails+Leeches	-7.60	1.46	1			
Neonates~Slugs+Snails+Leeches+LnEarthworms	-6.41	2.65	1			
Neonates versus environmental variables						

Neonates~Var7+LnVar9	-14.91	0.0	1	0.64	0.92	0.93
Neonates~Var7+LnVar9+LnVarZ	-13.02	-1.89	1			
Neonates~Var7+Var8+LnVar9+nNVarZ	-11.02	-3.89	1			
Neonates versus environmental variables and prey abundances						
Neonates~Var7+LnVar9	-14.92	0.0	1	0.64	0.97	0.93
Neonates~Snails+Var7+LnVar9	-13.45	-1.45	1			
Neonates~Snails+Slugs+Var7+LnVar9	-12.12	-2.80	1			
Neonates~Snails+Slugs+Var7+LnVar8+LnVar8	-10.38	-4.54	1			
Neonates~Snails+Slugs+Lnearthworms+Var7+LnVar8+LnVar9	-8.98	-5.94	1			
Neonates~Snails+Slugs+Lnearthworms+Var7+LnVar8+LnVar9+LnVarZ	-7.20	-7.72	1			
Neonates~Snails+Slugs+Leeches+Lnearthworms+Var7+LnVar8+LnVar9+LnVarZ	-5.27	-9.65	1			

6.1.5 Discussion

In general, most of the reproductive phenology observed in *Ninia atrata* followed the typical patterns reported in tropical snakes. First, the early male maturation at smaller size than females agrees with the common trend among oviparous dipsadid species with small or medium-sized. (Parker & Plummer, 1987, dos Santos-Acosta, *et al.,* 2006, Pizzatto, *et al.,* 2008, Rebalato, *et al.,* 2016). Particularly, Goldberg (2004) reported to its related taxon *Ninia maculata* the same trend in which the smallest spermiogenic male was 179 mm SVL, and the smallest vitallogenic female was 190 mm SVL.

Second, the intersexual divergence in the reproduccion cycles in *Ninia atrata*, in which individual sexual cicles between sexes is asyncronic, whereas at population level the reproduction cycle is seasonal semisynchronous, and this agrees with the patterns observed in several tropical snakes from diverse phylogenetic histories (e.g. Sibynomorphus spp., *Atractus reticulatus, Drymobius margaritiferus, Dipsas albifrons*, *Mastigodryas melanolomus, Micrurus lemniscatus*, among others) (Goldberg, 2006, Pizzatto, *et al.,* 2008, Marques, *et al.,* 2013). Also, *Ninia atrata* seasonal reproductive cycle showed a close relationship with the marked climate seasonality of the study area, prey abundance and hatchling survival. For instance, the greatest recruitment peak took place on mid-dry season, which coincides with the increase of snails' abundance. On mid-rainy season the greatest recruitment dearth was observed, which coincides with decline of the snails' abundance (Figure 5). Likewise, the remarkable decrease of neonates during the bad years highlights their high sensitivity to extreme climate changes, and supports the stated by Shine (2003), who argues that even in tropics seasonal reproductive cycles would be favored because they reflects the variability of operative environment factors, as well as the temporal shift on the reproductive trade-off.

Third, the presence of several vitollogenic-ovigerous females during the reproductive season, the constant recruitment of neonates through all year, the highly frequent mating evidence through all year independently of the climatic season, and the precense of previtallogenic females with sperm into the oviduct and infundibulum observed in *Ninia atrata*, agrees with trends of numerous tropical snakes (e.g. *Erithrolamprus aesculapii, Erithrolamprus bizona*, *Mastigodryas bifossatus*, *Tropidonophis mairii,* among others), in which multiple clutches, high mating frequency and continuous sperm production characterized their reproductive phenology (Marques, 1996, Brown & Shine, 2002, Goldberg, 2004; 2006).

In contrast, the body size-fecundity relations observed in *Ninia atrata* took distance from typically correlation between snout–vent length and reproductive output in tropical snakes (Miranda, et al., 2017). In *Ninia atrata* SVL showed to be a poor morphological predictor of fecundity. Particularly, the SVL was only significantly related with eggs´ mass, presumably reflecting physical constraints on clutch volume (Shine, 1991). On the contrary, body mass showed to be a better morphological predictor on both sexes, being this trait persistently selected in all regression models assessed. Especially, males body mass have the strongest contribution (> 50%) on sperm production, being the unique trait selected among the reproductive intrinsic traits evaluated. Similarly, females body mass in all regression models evaluated always occupied the second or third place of importance (≤ 20%), being displaced by traits such as secondary follicles number, stomach bolus volume, or fat body area.

In the same way, prey abundance and food intake showed to be a crucial variables that contribute to reproductive output in *Ninia atrata*. Particularly, the high frequency of vitallogenic or ovigerous females with stomach content as well as great importance of food intake in the secondary follicules and sperm production rathern than fat bodies or SVL, highlights the importance of these variables in the reproductive cycles.

All of the evidence suggests that *Ninia atrata* employs an income breeding strategy (Jönsson, 1997) in order to compensate the demands of reproduction and maximize fitness. This result agrees with feeding patterns observed in which largest females have significant higher values of stomach bolus volume than largest males, the presence of intersexual dietary divergence, and the notable disparity in feeding rates between sexes (See epigraph 6.2). Moreover, unlike other tropical snakes which seasonally have a shift in their reproductive strategy (from capital breeding to income breeding or vice versa, e.g., *Tropidonophis mairii*) *Ninia atrata,* despite the huge climatic variability that it was exposed due to ENSO phenomenon; has maintained the same reproductive strategy.

Income breeders are considered rare among ectotherms because of high energetic “cost” associated to maintain all the muscles and organs needed to sustain their highly-active mode of feeding (Bonnet, et al., 1998). However, *Ninia atrata* populations studied in the oil palm plantations have huge amount of preys available all year around, allowing them to reduce their acquisition energetic costs without exceed the energetic cost that would have to be expended in reproduction or any other activity (See epigraph 6.2). Hence, income breeding strategy observed in this population could be strongly influenced by habitat, however, more empirical data is sorely needed in order to elucidate whether reproductive strategy observed switches with habitat type, or it is a conservative life history trait of the species.

Finally, macroscopic reproductive traits showed to be an inaccurate proxy to reproductive activity in both sexes of *Ninia atrata*. Particularly, testicular volumen and SSK don’t shown asociation with sperm production. Likewise, oviduct distal width and the presence of chin tubercles exhibited a wide variance that makes it difficult for an accurate maturity size determination. The accuracy of the macroscopic reproductive traits as proxy of the reproductive cycle evaluation has been questioned (Mathies, 2011, Braz, et al., 2014). In fact, it has been observed that histological analysis invalidates macroscopically determined maturity in fishes and fossorial snakes (Vitale, et al., 2006, Braz, et al., 2014). Nonetheless, this topic has been poorly explored in snake reproductive studies due to historical and wide spread use of macroscopic reproductive traits in comparisons between different studies (Pizzato & Marques, 2006, Pizzatto &

Marques, 2007). Therefore, with the aim of future comparison between *N atrata* populations or related taxa, I recommend to employ a histology assessment seeking to avoid spurious results that could distort the relationship between reproductive cycle, environmental factors and reproductive trade-off.

6.1.6 Literature cited

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6.2 Life is uncertain, eat dessert first: feeding ecology and prey-predator interactions of the coffee snake *Ninia atrata*

6.2.1 Abstract

Despite of foraging and prey-predator interactions have been considered as prime ecological and evolutionary forces in snakes, the feeding ecology of the semifossorial tropical snakes has been poorly studied due to its cryptic habitats and elusive behaviors. This study explore the effects of sexual dimorphism, prey-predator interaction and climatic variability (ENSO effects) on abundance and feeding rate of the semifossorial snake *Ninia atrata*. As results, the *Ninia atrata* abundance varaibility observed was strongly explained by snail’s abundance more than other dietary items. Also, this prevalence suggests that phylogenetic inertia more than the ecological factors determines its feeding preference. Conspicuous intersexual dietary divergence was observed supporting the hypothesis of the sex-specific targets for maximum feeding rates. Finally, ENSO phenomenum promoted a notable decline in *Ninia atrata* abundances and its food intake, which was related with prey availability and abundance, as well as a strong variability on their BCI values. Therefore, due to the high sensitiveness of *Ninia atrata* it could be seen as indicator organism of the envirinomental changes at oil palm agroecosystems.

Key words: Abundance, El Niño–Southern Oscillation, Neotropical snake, Oil palm plantations, Snail-eating snake, Seasonality**.**

6.2.2 Introduction

Drivers of population abundance and density are one of the central issues both for ecology and for conservation. Prey availability has been proposed as one of the crucial explanatory factors of abundance and density variance as well as demographic processes in wild populations, based on results from experimental manipulation of food supplementation (Brown & Munger, 1985; Beissinge, 1990), as well as correlation evidence (Fitch, 1975, Ford & Pitelka, 1984, Shine & Madsen, 1997). Therefore, feeding ecology has been broadly studied, particularly in vertebrates and insects as the main model organisms. Among vertebrates, snake feeding has attracted the attention of many researchers because they exhibit amazing adaptations to overpower their prey, such as constriction or envenomation (Lillywhite, 2014).

Hundreds of papers published on this topic have built a framework that suggest that foraging and prey-predator relationnships are major ecological and evolutionary forces in snakes’ ontogeny and phylogeny (Mushinsky, 1987). However, most of feeding ecology knowledge has been developed from temperate-zone taxa, even though the highest snake richness is concentrated in the tropical region, and most snake lineages have reach their greatest diversity in the tropics (Ávila, *et al.,* 2006, Whitaker & Shine, 2000).

Recently, the historical disparity between the number of feeding ecology studies on temperate and tropical zones has been reduced. Particularly in South America, in last two decades, the understanding about the snake feeding ecology has been expanding and now we have increase knowledge about food types and their relative amounts in the diet, seasonal food intake, ontogenetic or sexual diet shift, and evolution of diet and microhabitat use (Marques & Puorto, 1998, Vitt, 1996, Valdujo, *et al.,* 2002, Ávila, *et al.,* 2006, Alencar, *et al.,* 2012, Gomes & Marques, 2012, Gaiarsa, *et al.,* 2013, Miranda *et al.*, 2017). Nonetheless, the feeding ecology of the fossorial and semifossorial tropical snakes continues to be poorly studied due to its cryptic habitats and elusive behaviors.

The semifossorial snake *Ninia atrata* (Hallowell 1845) is the most widely distributed species of the genus Ninia in South America spreading from western

Panama to Northern Peru (Angarita-Sierra 2014). This species has a high tolerance to disturbed or transformed habitats such as oil palm plantations and annual crops in which *Ninia atrata* is the most common snake species in these monocultures (Angarita-Sierra 2015). Nonetheless, feeding ecology and prey-predator interactions have remained unknown. Here, a description is provided for the feeding ecology of *Ninia atrata*, exploring the influence of sexual dimorphism in diet. Likewise, prey-predator interactions and climatic variability was evaluated as drivers of snake abundance. Therefore, the following questions were assessed: I) Does is sex more than body size which explains the variation in diet? II) How is the relationship between body size, feeding rate and climatic variability? And III) How the prey abundance and climatic variability influence the abundance of *Ninia atrata* populations that inhabit oil palm plantations?

6.2.3 Methods

6.2.3.1Study area and data collection

Ninia atrata specimens were collected on a monthly basis at oil palm plantation of PALMASOL S.A. located on high savanna plateaus of the Llanos Orientales of Colombia in vereda La Castañeda, municipality of San Martin, department of Meta–Colombia (3°31´46, 6” N; 73°32´15,3” W) (Figure 1). This region has monomodal climate in which rainy season occurs between April to mid–half of November, and dry season begins in the second half of November till March. Climatic variability was categorized as good years that represent the sampling period (from Aug 2014 to December 2015) without El Niño–Southern Oscillation (ENSO) effects, and bad years when the sampling period (from Jan 2016 to February 2017) took place under ENSO effects.

Sampling was conducted in four production batches removing piles of palm leaves from 7:30h to 17:30h during 3 days from August of 2014 to June of 2017. Due to logistic constrains, and only in two occasions (Sept 2014 and May 2015), no sampling was taken. After the removal of palm leaves piles, the ground was raked up 5 to 15cm deep. Immediately, prey items sighted were recorded and all snake individuals were hand–captured and put in cloth bags. Prey availability (PA) was defined as the ratio of sampling period that a prey is present in a microhabitat (Equation 1).

$$PA = \frac{Pj}{Pj + Abj} \times 100$$

Equation 1. Prey availability proportion (Pryor, 2008). Where PA is prey availability proportion, *P* represent the times number when the *j* prey item was present and *Ab* represents the times number when the *j* prey item was absent.

All snakes obtained were measured (snout–vent length=SVL; Tail length=TL) with scale-tape and weighed with a Pesola® spring scale. Likewise, health conditions, sex, umbilicus scar, and secondary sexual traits in males were recorded. Examination of gonads and eggs were recorded using palpation, and through contrast light upon the snake body from dorsal to ventral surface. At each period of sampling, environmental temperature and relative humidity, as well as temperature and relative humidity of the microhabitats were recorded using thermo-hygrometers model EBI 20-TH1 Ebro®. All snake collected were preserved with 10% neutral buffered formalin and later transferred to 70% ethanol for permanent storage. Also, museum specimen of *Ninia atrata* (*n*=63) from same locality or collected in oil palm plantations form Orinoquian region were included in the study. A total of 170 digestive tracts were dissected and its stomach contents were examined. Only intact preys found were determined to the minimum taxonomic resolution possible and they were considered in dietary analysis.

The soft anatomy measurements such as head length and width, stomach bolus, fat bodies area, and prey sizes were taken through digital picture using Image–J software. Following the procedures of Ávila, *et al.,* (2006) stomach bolus volume was estimated employing Equation 2, and resource partitioning by sex were estimated employing Equation 3. Fat body areas were calculated as the sum of the all polygons resultant of the fat bodies attached to digestive tract of each individual. Also, body condition index (BCI) was estimated employing Equation 4. Diet breadth was estimated using a Chi–square ($\chi 2$) test and G–test with William´s correction in the polytomic cases (Saikia 2012).

$$V = \frac{3}{4}\,\pi\left(\frac{w}{2}\right)^{2}\left(\frac{l}{2}\right)$$

Equation 2. Ellipsoid formula to calculate prey volumes and stomach bolus. Where V= Stomach bolus or prey volume estimated; *w*= prey width and *l*=prey length.

$$\phi_{ij} = \frac{\sum_{i=1}^{N} P_{ij}P_{ik}}{\sqrt{\sum_{i=1}^{N} {P_{ij}}^{2}\ \sum_{i=1}^{N} {P_{ik}}^{2}}}$$

Equation 3. Resource partitioning for both numeric and volumetric measures of prey, considering sex and developmental states. Where p represents prey category *i, n* is the number of categories, and *j* and *k* represent the two groups being compared. Values range from 0 to 1 being 0 no overlapping and 1 complete overlap.

$$BCI = Log(w) \times (\frac{\hat{W}}{Log(SVL)})^{S}$$

Equation 4. Body condition index. Where BCI is the Body condition index estimated. w= weight, SVL= snout–vent length, Ŵ= weight mean and s= Slope of the linear regression between Log (SVL) and Log (w).

6.2.3.2Statistical analysis

Differences in the absence/presence of stomach contents, snake abundance variability related with climatic years, prey availability, variation and stomach content states (empty, unidentifiable, partially identifiable, and completely identifiable) between males and females were assessed using Chi–square (χ^2) test or *t*–test. Correlation between stomach bolus volume (mm^3) and SVL was performed using the Spearman coefficient with P<0.05 as criterion for independency significance. Likewise, the relationship between body size, feeding rate and prey abundance was evaluated using a linear regression analysis and ANCOVA.

Prey–predator interactions were assessed through a multiple regression analysis. Hence, the following steps were carried out. First, the following abiotic and biotic variables were considered: temperature and relative humidity of the environment and microhabitat (Var1 and Var2), prey counts at each sampling occasion (Var3=snails, Var4=earthworms, Var5=slugs, Var6=leeches, Var7=Total food), and microhabitat quality (Var8= Height of palm leaves piles). All these variables were Ln–transformed following equation 5 seeking a smoothen distribution

$$Ln(variable - (\min(variable) - 1)$$

Equation 5. Ln-transformed variables. Where Ln means natural logarithm and *min* represent very small positive number.

Second, assumptions of normality, autocorrelation, and homoscedasticity were evaluated using Kolmogorov–Smirnov's test, Durbin–Watson test and Breusch–Pagan test, respectively. Third, multicollinearity between the variables previously named was tested using statistical technique of variance inflation factor (VIF) with a threshold of 10. Fourth, to select "best" regression model based on the variables evaluated the Akaike Information Criterion was employed (AIC) (Akaike, 1973). A difference in AIC values (∆AIC) larger than 2 indicates a real difference between models in fit to the data (White and Burnham, 1999)

Finally, the contribution of all the independent variables to the regression model was assessed using the hierarchical partitioning method (Chevan and Sutherland, 1991). All statistical analyses were done using the software Rwizard 2.3 (Guisande–Gonzáles, *et al.,* 2014) and the following *R* packages hier.part (Walsh and MacNally, 2015), nortest (Gross, 2015), lmtest (Hothron, et al., 2017), and usdm (Naimi, 2015).

6.2.4 Results

During the sampling period 425 specimens of *Ninia atrata* were caught (males=209; females=216). A total of 79 prey items were completely or partially identifiable where snails was the most frequent prey category (34.17%; *n*=27) followed by slugs (30.37%; *n* =24), earthworms (27.87%; *n* =22) and leeches (7.60%; *n* =6) (Figure 11A). Taxonomic prey diversity is composed by four families, three genus, three species and two morphs species (Table 3). Particularly, snails were easily identifiable because in most cases their shells remained intact within the digestive tract. This result suggests that feeding behavior of *Ninia atrata* consists of swallowing the whole snail including its shell.

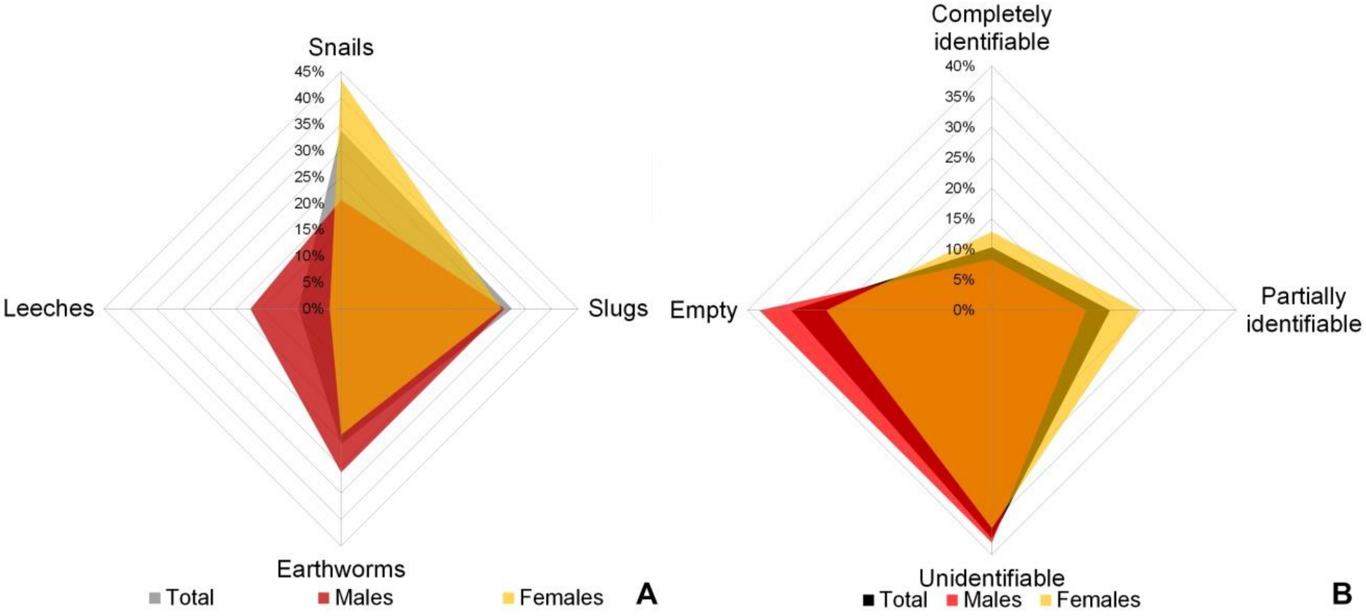

Figure 11. Radial plot depicting the prey preference and stomach content states from specimens dissected. A) Prey items frequency by sex and total sampling. B) Stomach content states frequency by sex and total sampling.

Table 3. Prey diet items of *Ninia atrata* population that inhabits an oil palm plantation from Llanos Orientales of Colombia.

Prey category	Order	Family	Genus	Species	N	Relative abundance
Snails	Stylommatophora	Subulinidae	Subulina	*Subulina octona*	15	20.5%
			Leptinaria	*Leptinaria unilamellata*	10	13.7%
Slugs	Stylommatophora	Veronicellidae	Sarasinula	*Sarasinula pleneia*	22	30.1%
Earthworms	Opisthopora	Rhinodrilidae		Morph 1	20	27.4%
Lecches	Hirudinea	Haemadipsidae		Morph 2	6	8.2%

Sex differences between absence/presence of stomach contents (χ^2= 0.014, *P*= 0.90, *n= 170*) and stomach content states (χ^2= 3.7147, *P*= 0.29, *n*= 170) were not statistically significant. In contrast, diet breadth between sexes showed significant differences in which females have a significant predilection for snails more than the remaining prey categories (χ^2= 9.1159, P= 0.028, n=170), exhibiting a moderately specialized diet. While males have moderately generalized diet, being slugs, earthworms and leeches its preferred preys (Figure 12). Nevertheless, the degree of resource partitioning is low showing an 84.34% overlap between sexes.

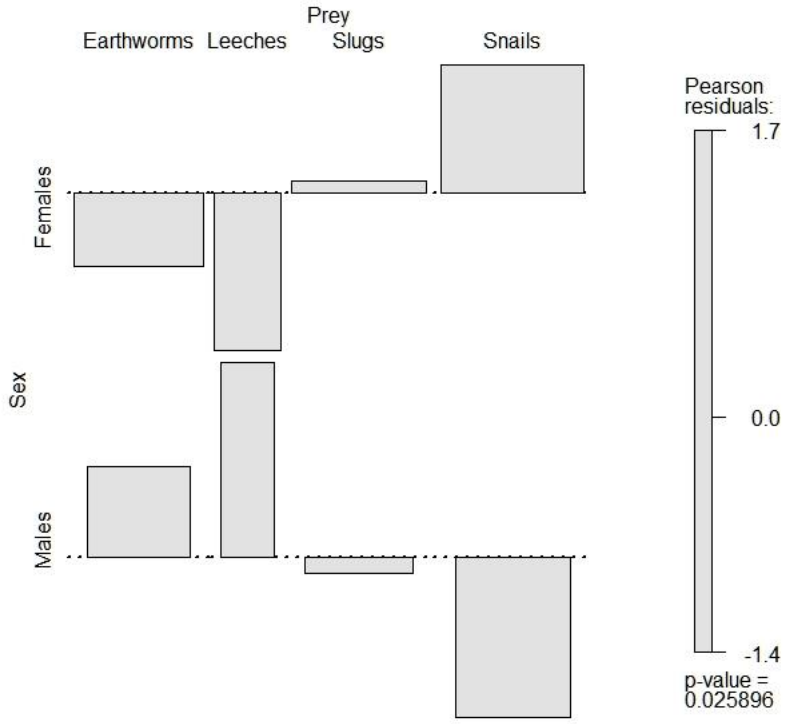

Figure 12. Diet breadth of *Ninia atrata* population that inhabits an oil palm plantation from Llanos Orientales of Colombia.

As expected, result analysis from the exploration of relationship between sexual size dimorphism, prey size and head size exhibited a differential association. Tail length (t= -3.1999, *P*= 0.0015, *n*=415) and weight (ANCOVA, P< 0.0001, *n*=231) were significantly different between sexes, being males lighter and with larger tails than the females. Meanwhile, head length (*t*= 0.2556, *P* =0.61, *n*=415) and head width (*t*= 0.82642, *P* =0.36, *n*=415) were related with SVL between sexes were not significantly different. Likewise, body size related to prey size does not showed significant correlation between sexes (R_{spearman}=0.10, *P*= 0.60, *n*=75). Also, when only the prey size ingested by each sex is considered no significant differences were observed either (*t*= -1.246, *P* = 0.22, *n*=72). Nonetheless, I explored the hypothesis that body mass rather than SVL explains the head dimensions dimorphism. Therefore, an ANCOVA analysis was carried out showing a significant differences between sexes, in which heavy females have largest and widest heads than males (ANCOVA, *n*=151, P< 0.001) (Figure 13). In contrast, body mass and prey size does not show significant correlation between sexes (R_{spearman}=0.10, *P*= 0.60, *n*=75)

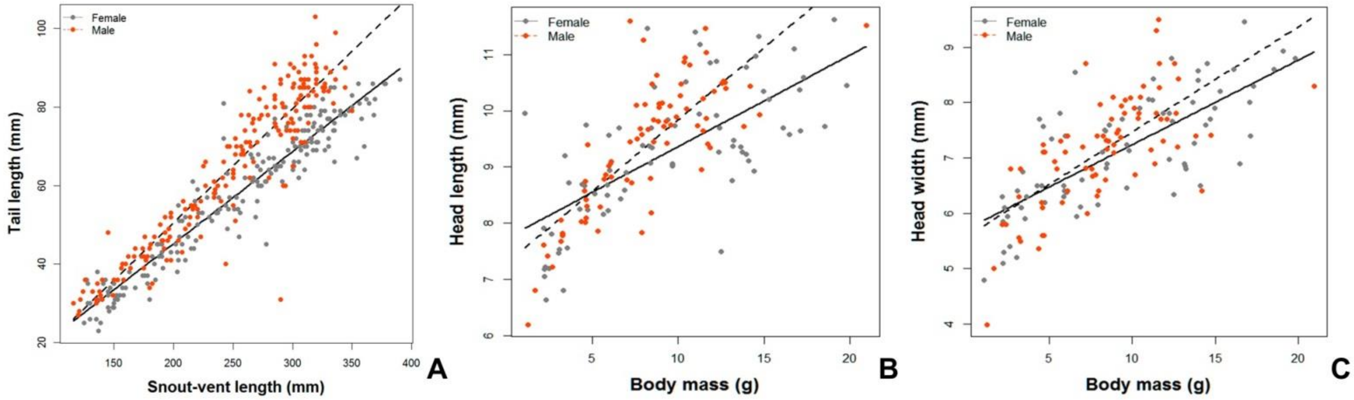

Figure 13. Sexual dimorphism in body proportions of *Ninia atrata* populations that inhabit an oil palm plantation from Llanos Orientales of Colombia. At equivalent body lengths or body mass A) Males (orange dots) have longer tails than do females (grey dots). B and C) Scatter plot depicting head proportions in which heavy females have largest and widest heads than males. See text for statistical tests of these sex differences.

On the other hand, most snakes had unidentifiable stomach content or empty stomach (61.08% *n* =124) (Figure 11B). Although more than half of the sample had stomach content (52.70%; *n*=107), the correlation analysis shows that stomach bolus volume has a significant correlation with snake SVL (R=0.69, *P*< 0.001, *n*=107), depicting that at higher SVL there is higher stomach bolus volume. Moreover, almost less than third part of the samples (38.91%; *n*=79) with complete or partial the stomach content identifiable had more than one prey item (range 2–6 prey items) and included up to three different prey categories.

Furthermore, when comparing stomach content between sexes, it was observed that largest female snakes had significant higher values of stomach bolus volume than largest males among the dissected sample (Males $_{\text{Highest scores}}$= 439.89─1,171.64 mm^3; $\bar{x}$=729.17 mm^3, *n*=5; Females $_{\text{Highest scores}}$= 1,172.59─1,346.96 mm^3; $\bar{x}$=1,322.31 mm^3, *n*=5; χ2= 171.49, *P*< 0.001, *n*= 10). Particularly, most gravid snakes (79.31%, *n*=29) present stomach content and high values of stomach bolus volume as well as more than one prey item in their stomach. Also, the degree of association between stomach bolus volume and fat body area have a differential correlation between sexes, in which females have a statically significant correlation (R $_{\text{pearson}}$=0.37; *P*= 0.017) whereas males does not (R $_{\text{pearson}}$=0.37; *P*= 0.39).

Notwithstanding, largest males have higher feeding rate than largest females (Figure 14). Particularly, males feeding rates tend to increase constantly with the increment of body length whereas females show stationary or low feeding rates stages (Figure 14A). Besides, a higher fat body area were recorded in females than males with significantly correlation between SVL and fat body areas (R $_{\text{spearman}}$=0.43; *P*< 0.001).

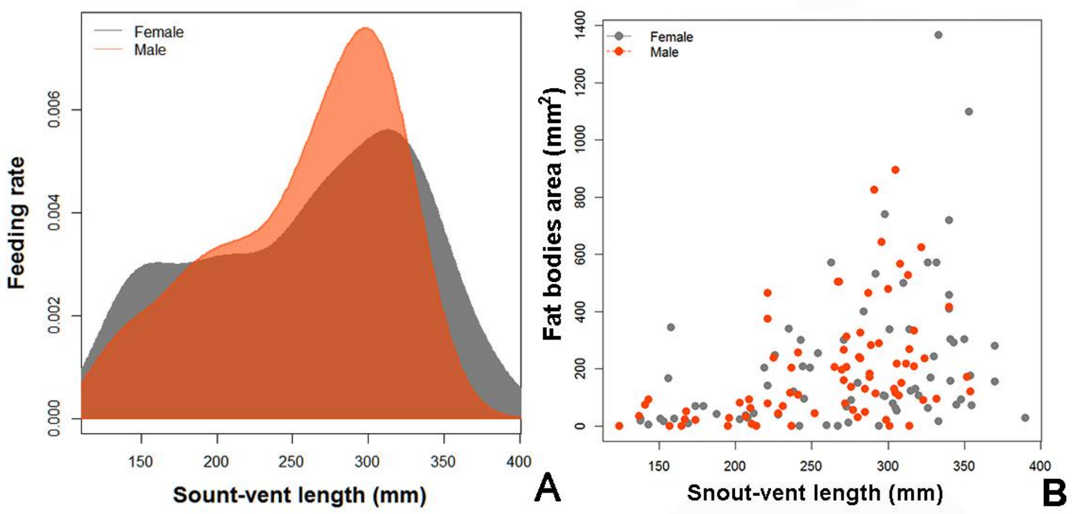

Figure 14. Relationship between feeding rate, fat body area, sex and snout-vent length. A) Feeding rate tend to increase constantly with the increment of the body size in males. In contrast, females show stationary feeding rates stages through their body size growth. B) Fat body area increase with the increment of the body size, being higher in females.

The climatic variability analysis revealed conspicuous temporal variation in the prey availability, snake abundance and feeding rate. First, of the total prey items (*n*= 9962) recorded, earthworms (79.34%, *n*= 7904) and snails (19.34%; *n*= 1927) were the most abundant preys through the sampling period, showing high values of prey availability (earthworms= 96.55%; snails= 100%). However, their abundances have high seasonal variability showing a significant difference between dry and rainy season (χ^2= 4025.1, P<0.0001, *n*= 9962). For instance, snails showed higher abundance during dry season while earthworms were abundant during rainy season (including good and bad climate years). In contrast, leeches (1.28%, *n*=128) and slugs (0.03% *n*=3) were the least abundant preys, showing moderate and low values of prey availability respectively (leeches= 71.42%; slugs= 7.14%). In the same way as earthworms, leeches showed high seasonal variability in which they are more abundant on rainy season than dry season (χ^2= 30.031, df= 1, P< 0.0001, *n*= 7904). Particularly, slug's availability and abundance show a contrasting result that disagrees with the prey frequency analysis in where they occupy the second relevance place in the diet of *Ninia atrata*.

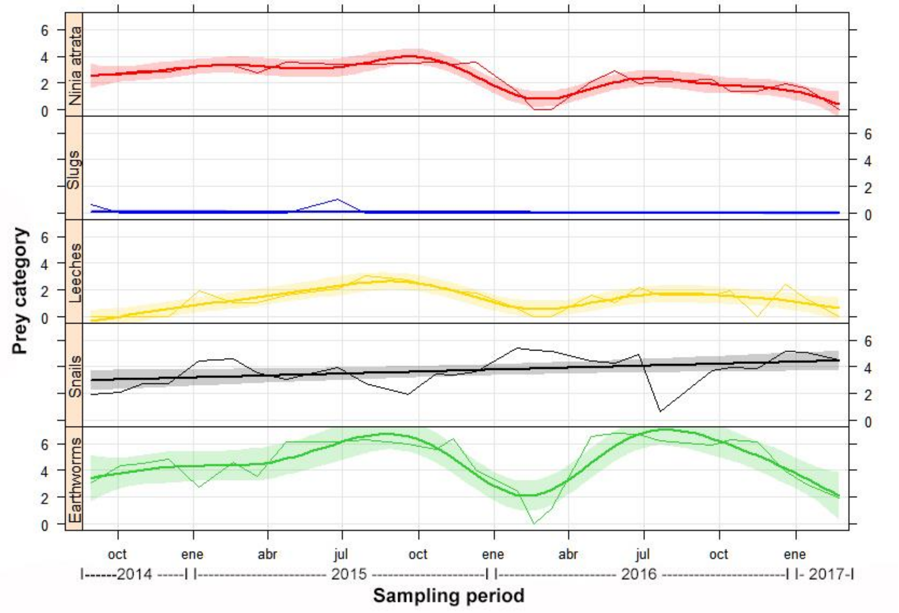

Figure 15. Temporal abundance variation of prey items and *Ninia atrata* population through sampling period. Scale of the Y axis represents the Ln-transformed abundance values using equation 4. Shaded

area represents 95% confidence intervals. Zigzag lines represent the Ln-transformed abundance values at each sampling period.

Second, as expected, ENSO phenomenon affected noticeably both prey and *Ninia atrata* abundance. Comparatively, between good and bad years the abundances of *Ninia atrata* exhibited enormous variability from 164 individuals during dry season of the good years, to 76 individuals during dry season of 2015-bad years, having two months in which neither snake was observed (February and March of 2016). Likewise, during the rainy season during ENSO effects a total of 61 snakes were observed. By contrast, during rainy season without ENSO effects a total of 124 were recorded. During dry season under ENSO effect the lower abundance of *Ninia atrata* were significant (χ^2 = 176.15, *P*< 0.0001, *n*=415) as well as number of snakes with stomach content between good and bad climate years (*t*= -4.6199, *P*< 0.001, *n*= 415). Similarly, earthworms, leeches (dry season) and snails (rainy season) also shown significant lower abundances in comparison with the same period in years without ENSO effect (χ2= 4015.6, *P*<0.0001, *n*= 9962) (Figure 15). In addition, the prey-predator abundance variability had shown high correlation between good and bad years. Particularly, snails (R_{snails}= -0.546, *P*= 0.003 *n*= 29) and leeches ($R_{leeches}$= -0.440, P= 0.019 *n*= 29), have close correlation with *Ninia atrata* abundance showing a similar temporal variation pattern.

Similarly, snakes body condition shown a visible seasonal pattern in which lowest values were recorded during dry season and highest values were recorded during rainy season (Figure 16A). The lowest BCI values are due to higher proportions of neonates than adults, as well as the records of large adults with low weights. At same time, ENSO effects caused a significant differences on the BIC values between good and bad years (*H*= 104.26, P< 0.0001). Particularly, during dry and rainy season of the bad years (2016—2017) BIC values were extremely low being almost twice lower than BIC values reported for the good year (Figure 16B).

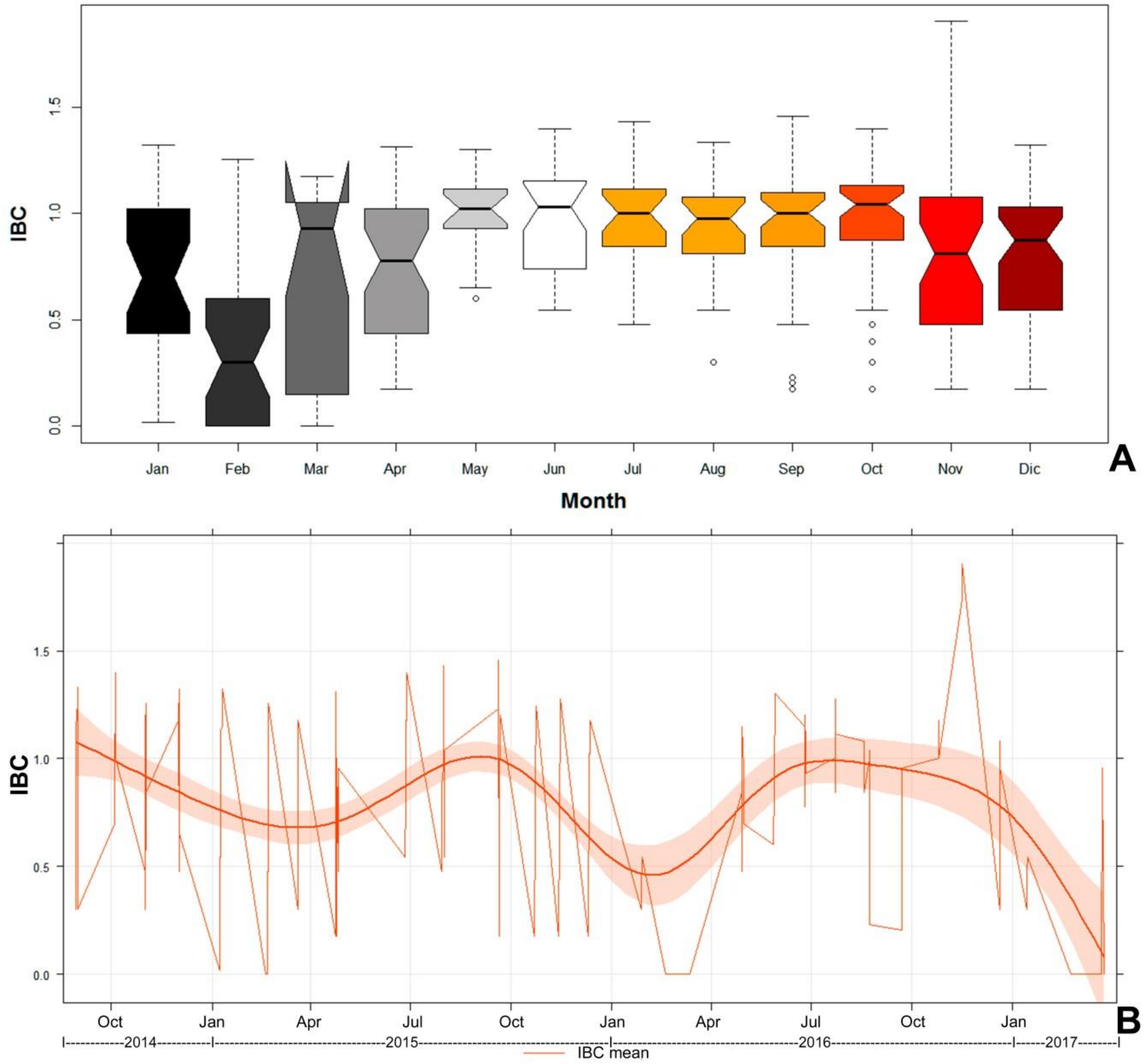

Figure 16. Climatic variability of Body condition index (BCI). A) Boxplot showing BCI variability summarized by month on entire sampling period. B) Time series showing BCI monthly variability through good (without ENSO effects) and bad (under ENSO effects) years.

Third, as expected, feeding rates were higher in months and years when preys were abundant ($R_{\text{good years}}= 0.529$, $P= 0.0045$ $n= 29$; $R_{\text{Bad years}}= 0.614$, $P< 0.001$, $n=29$), nonetheless, snake abundances and feeding rate were significantly higher in good climatic years rather than bad years. Despite huge differences observed on prey abundance between good and bad years, feeding rates were not statistically different (t= 1.752, df= 24.018, $P= 0.092$,), suggesting that the feeding rates trend is maintained independently of climatic year (Figure 17).

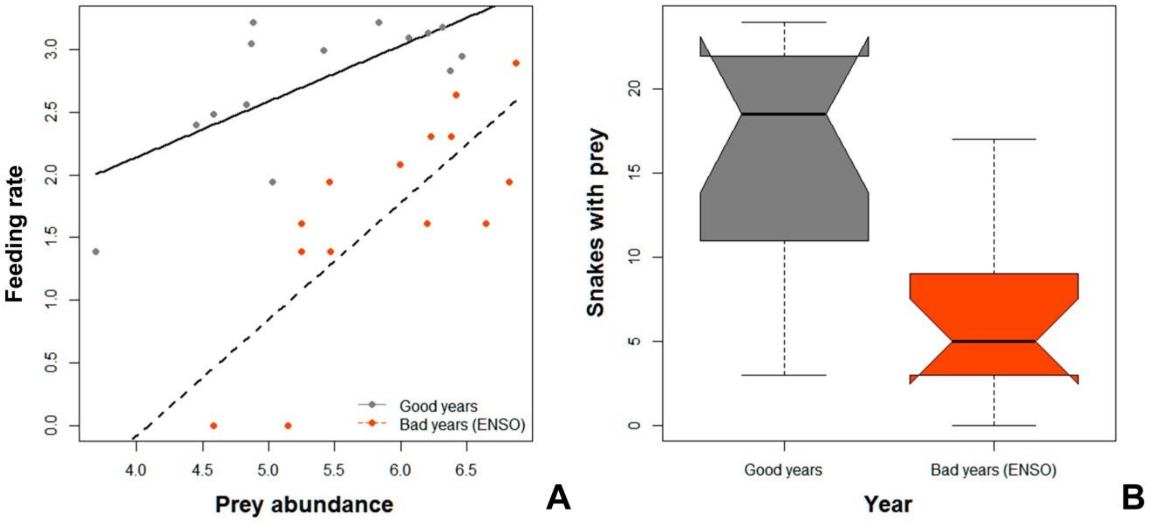

Figure 17. Temporal variation. A) Relationship between feeding rate and prey abundance (Snails, slugs, earthworms and leeches). B) Comparison among snakes with prey between good and bad climate years. All variables were Ln-transformed.

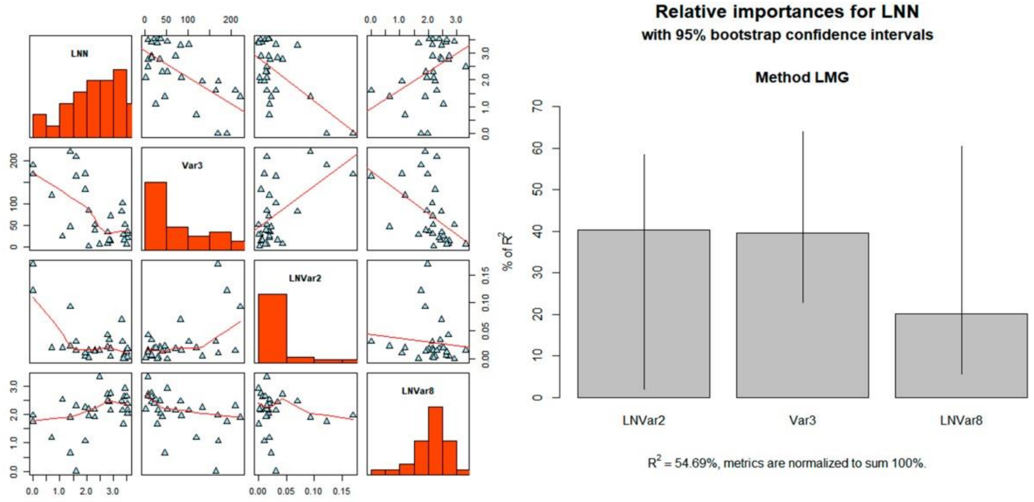

Figure 18. Matricial plot of the "best" regression model and variable contributions. A) Matricial plot depicting the "best" regression model that explains the abundance variability of *Ninia atrata* observed. B) Individual contributions of the variables selected through variance inflation factor (VIF). LNN= Ln-transformed *Ninia atrata* abundance. LnVa2r= Ln-transformed microhabitat temperature/relative humidity, Var3=Snails, and LNVar8= Ln-transformed height of piles palm leaves.

Finally, regression analysis models results clearly conclude that between the eight abiotic and biotic variables evaluated snails, environment temperature/relative humidity, and height of palm leaves piles were the variables that more contributed to explain the abundance variability of *Ninia atrata* (Figure 18). However, between these selected variables the "best model" is composed by snails and leeches which explain the 57.50% of the snake abundance variability observed (R^2= 0.58, P< 0.0001).

Table 4. Multiple regression models. Akaike Information Criterion (AIC) employed to select the "best model" that relates the fluctuation in prey availability, climatic variability and the abundance of *Ninia atrata.* LNVar1= Ln-transformed environmental temperature/relative humidity, Var3=Snails, Var4=earthworms, Var5=Slugs, Var6=Leeches, and LNVar8= Ln-transformed height of piles palm leaves. Nor.test= Kolmogorov–Smirnov's test for normality, Hom.test= Breusch–Pagan test for homoscedasticity, and Aut.test= Durbin–Watson test for autocorrelation

Model	AIC	dAIC	Nor.test	Hom.test	Aut.test
N~Var3+LNVar2+LNVar8	-13.38	0.0	0.72	0.93	0.005
N~Var3+LNVar2+LNVar8+Var7	-12.06	-1.22			
N~Var3+LNVar2+LNVar8+Var7+LNVar1	-10.35	-3.03			
N~Var3+LNVar2+LNVar8+Var7+LNVar1+Var6	-8.44	-4.94			
N~Var3+LNVar2+LNVar8+Var7+LNVar1+Var6+Var5	-6.45	-6.93			

6.2.5 Discussion

Ninia atrata abundance variation observed was strongly explained by snail's abundance more than any other dietary items. This result agrees with prey preference observed and disagrees with the reported by Cadle and Greene (1993), Savage (2002), Lynch (2015) and Rojas–Morales et al. (2017) who indicates that *Ninia atrata* is an earthworm–eating snake. In fact, earthworms represent only 26.92% of its diet and ranking third among the four food categories recorded, despite to be the most abundant prey during the whole sampling period. In contrast, gastropods represent 65.38% of the *Ninia atrata* diet, being snails the major dietary component. Therefore, I concluded that *Ninia atrata* is a snail–eating snake rather than an earthworm–eating snake.

Particularly, slug's availability and abundance show a contrasting result that disagrees with the prey frequency analysis in which they occupy the second relevance place in the diet of *Ninia atrata*. This result suggests two possibilities. First, the sampling technique employed to detect preys was inappropriate to slugs, or second, *Ninia atrata* forage slugs in others microhabitats not sampled in this study. Therefore, it would be expected that with a suitable sampling technique or wider microhabitats sampling, the slug's abundance it could explain on similar way as snails the *Ninia atrata* abundance variability.

The prevalence of gastropod preys in the *Ninia atrata* diet supports the evolutionary hypothesis stated by Sheehy III (2012) which asserts that Dipsadine snakes experienced a dietary shift and adaptive radiation that made them converge into a gastropod specialized diet. The genus Ninia (plus Chersodromus) as well as genus Dipsas (*sensu stricto*) are sister clades of Dipsadini tribe. These three clades are related by their gastropod specialized diet, but also, they can be distinguished by their feeding behavior. Whereas Dipsas snakes extract snails using alternating movements of their mandibles, and Dipsadini tribe snakes extract snails by dragging and snagging or wedging the shell on surface irregularities (Sheehy III, 2012). Snakes of genus Ninia swallow the whole snail, including its shell. Therefore, this evidence suggests that phylogenetic inertia (Gould and Lewontin, 1979) more than the ecological determinants, are the main factors that influence *Ninia atrata* diet preference. As a consequence, we would expect that *Ninia atrata* populations from diverse natural land covers or oil palm plantations outside the Colombian Orinoquia region show a similar dietary composition in which gastropod represents the main food category.

One predication of foraging theory is that body size may determine the kind and size of prey (Krebs, 1978). However, lack of correlation between SVL and prey size, the absence of sexual dimorphism in head size related to SVL, and the significant differences in prey preferences between sexes observed in *Ninia atrata,* suggest that sex rather than body size, explains diet variation in this taxon. Moreover, the conspicuous intersexual dietary divergence observed, supports the hypothesis of sex–specific targets for maximum feeding rates (Brown and Shine, 2017). Particularly, the feeding rate pattern relative to body size showed a divergent energetic requirements between sexes, suggesting that the female's specialized diet causes a lower food intake frequency than males throught the same increment of body size. Indeed, females showed noticeable differences in the feeding rate behaviour at same body size than males, being females faster than males when they are neonates, slow when they are juveniles and slower than males when they are adults (Figure 14).

Also, this intersexual dietary pattern supports the hypothesis of the dimorphic niche adaptation (Shine 1989), and suggest, that the reproductive requirements could be one of the main mechanism that provoke sexual dimormphism in *Ninia atrata*. Females of *Ninia atrata* with SVL that ranges between 125–270 mm are previtellogenic (Angarita–Sierra unpublished data), that means that energy gain from food intake is allocated in growth and fat reserves rather than reproduction requirements. When females exceeds 270mm SVL, they star their reproductive activity (vitollogenic, ovigerous, or both stages) as well as a second greater increment of food intake. Unlike other tropical snakes that cease their food intake when they begin their reproductive activity spending all their fat reserves in reproduction (capital breeder, Shine and Madsen, 1997), *Ninia atrata* females adjusts its food intake concurrently with reproductive requirements, without reliance on storage (income breeder, Jönsson, 1997). This allows them a constant growing during their reproductive stages, reaching high stomach bolus volumes and fat body areas.

On the contrary, males exhibited a constant increase of the feeding rate with the increment of the body size, but uncorrelated with the fat body reserves. This result suggest that, due to that *Ninia atrata* males exhibiting a striking early sexual maturity (over 145mm SVL, Angarita–Sierra unpublished data) their reproduction requirements pushing them to have a high food intake feeding from a wide range available preys in order to gain energy and spend it to growth and reproductive activities. As consequence, they exhibit generalist diet.

On the other hand, the food intake pattern observed suggests that feeding energetic costs of *Ninia atrata* populations inhabiting oil palm plantations does not exceed the energetic cost that would have to be expended anyway in other activities. Therefore, *Ninia atrata* can be considered as Type I predator according with Schoener (1969):

"…*A Type I predator is assumed to passively locate its prey by scrutinizing an area surrounding its vantage point and to be programmed for going after an item or not on the basis of that item's size and distance. While watching for items to enter its possible field of prey capture, the predator is concurrently carrying on* *other important activities such as maintaining a territory, grooming, looking out for predators, and monitoring potential mates…*".

Hence, Schoener catergorization helps to explain the presence of more than one prey item in the stomach contents, as well as a positive correlation between snake body size and stomach bolus volume in *Ninia atrata*. However, this catergorization does not satisfy the sex dimorphism observed in *N. atrata* in which body mass rather than SVL explain that females have largest and widest heads than males.

Usually, sex size dimorphism of the head seen in snakes (e.g., *Geophis nasalis*, *Thamnophis sirtalis, Coluber constrictor*) has been explained based on the hypotesis that larger head sizes evolved as an adaptation to allow ingestion of larger prey (Shine, 1991). This hypotesis is plausible whether the relationship between maximum prey size and gape size is correlated with body length (King, 2002). However, these assumptions does not fit with the *Ninia atrata* population assessed, because it do not shown significant differences between prey size ingested and sexes, which suggest equal gape–size between sexes. In addition, the relationship between body length and head size are not significantly different between sexes.

As alternative, these differences between sexes may be explained as a phenotypic plasticity response due to prey size availability in the microhabitats, as well as experience of different selection pressures on head dimensions as consequence of the divergence in the prey preferences between sexes. Diet–induced phenotypic plasticity on trophic structures has been reported in fishes (Day, *et al.,* 1994), reptiles (Forsman, 1991) and mammals (Myers, *et al.,* 1996). Particularly, the experimental study on *Nerodia sipedon* developed by Queral–Regil and King (1998) demostrated a significant relationship between prey size, food intake, body mass and snakes head dimensions, suggesting that phenotypic plasticity in these traits may contribute to patterns of morphological variation observed in nature, including sex dimorphism.

Therefore, high preference of snails in the *Ninia atrata* female's diet could promote their big size head development as a consequence of the constant amount of bulky and rigid snail shells ingested. In contrast, the wider prey preferences observed in males allows them to feed mostly of soft–body preys that require minor head size modifications. However, future experimental studies must be addressed to test whether intersexual ditary divergence causes the sexual size dimorphims observed in *Ninia atrata.*

According with the Colombian Institute of Hydrology, Meteorology and Environmental Studies the El Niño ENSO phenomenom recorded on 2016 was the strongest of the last 20 years (IDEAM, 2016). Especially, this climatic event had a deep impact on high savanna plateaus of the Llanos Orientales of Colombia causing elevated high temperatures and low moisture during dry season, and a deficiency of rainfalls during rainy season.

This extreme climate promoted a notable numerical response on number of snakes with stomach content as well as BCI values during bad years , which was strongly correlated with the decline of prey abundance (mainly snails and leeches), showing a buttom–up effect driven by El Niño ENSO phenomenom. These results clearly agrees with Dunham *et al.* (1989) hypotesis whom states that changes on operative enviorenment of ecthoterms directly influence indiviual time and mass–energy allocations, which in turn influence population size and its vital rates (Beaupre and Douglas, 2009). However, despite of theses hard conditions within bad years the feeding rate maintained the same trend observed during the good years, suggesting that prey abundance or availability decline does not influence the way in *Ninia atrata* takes its food.

As expected, the changes on the environment temperature and relative humidity were relevant to explain the abundance variability of *Ninia atrata* because they are a direct indicator of the constraint environmental conditions in which *Ninia atrata* inhabit, as well as part of the main climatic variables altered during ENSO episodes. On the contrary, height of palm leaves piles is an abiotic variable that depends on oil palm productivity, which ca be considered as an anthropogenic factor. The height of palm leaves piles depends on the plantation pruning cycle, which in turn depends on fructification productivity of the palms. Given that water deficit is the main constraints that affect vegetative growth, fructification physiology, and oil extraction rate (Mejía, 2000), during bad years, the high temperatures and deficiency of rainfalls causes a drop on fructification productivity and pruning rate. These changes in the microhabitat quality of *Ninia atrata* inducing a notable reduction in its abundance as a consequence of the decrease on height of palm leaves piles.

Similarly, ENSO effects have been reported in insects (Holmgren, et al., 2001), mammals (Jaksic, *et al.,* 1997) and tropical marine reptiles populations (Laurie and Brown, 1990). Nonetheless, tropical mainland animal populations has been lackly explored. Therefore, the results of the present study contribute to our understanding of the mechanism that relates annual seasonality, climatic extremely variability and prey–predator interactions. Besides, given the high sensitiveness of *Ninia atrata* to changes of the operative environment variables, this species could be seen as indicator organism of the environmental fluctuations at oil palm agroecosystems.

6.2.6 Literature cited

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6.3 Repertoire of antipredator displays in the semifossorial snake *Ninia atrata*

6.3.1 Abstract

Snake antipredator displays have an important relevance on the conflict snake-human due to it could induce intense feelings in people and provoke the intentional killing of snakes. However, antipredator displays have been poorly studied in most of semifossorial snakes. The genus Ninia is not the exception, among the thirteen nominal species of the genus only five have occasional records. Therefore, in this chapter the antipredator behavior *N. atrata* was assessed exploring the effects of ontogeny and sex, based on simulations of predator attacks in natural environment. As results, 13 antipredator displays were recorded, as well as three combined antipredator displays and one social response. In general, *N. atrata* follow a general pattern of hierarchical decision making when a predator stimuli is detected: retreat, passive deterrents and aggressive defense. Also, the behavioral patterns observed were not associated with the stage of maturity or sex. Perhaps antipredator response of *N. atrata* is more correlated to the phylogeny and habitat use rather than the intrinsically biological features. Nonetheless, complementary field and laboratory studies are needed to understand the behavioral responses patterns related with body size and sex as well as behavioral convergence between related taxa that inhabit the same biogeographic units.

Key words: Aggressive defense, Hierarchical responses, Predation, Oil palm plantations, Snail-eating snake, Passive deterrents.

6.3.2 Introduction

Snake antipredator displays have an important relevance on the conflict snake-human due to it could induce intense feelings in people and provoke the intentional killing of snakes. However, antipredator displays have been poorly studied in most of semifossorial snakes. The genus Ninia is not the exception, among the thirteen nominal species of the genus only five have occasional records (Angarita-Sierra & Lynch, 2017).

The semifossorial snake *Ninia atrata* is a widespread Neotropical species that ranges from western Panama, Colombia, Ecuador, and Venezuela to Trinidad and Tobago, at altitudes from sea level to 1000 ma.ds.l. (McCranie & Wilson, 1995; Savage, 2002, Angarita-Sierra, 2009; 2014). *N. atrata* inhabits leaf litter in almost all habitats, including the Amazonian and Chocoan rainforests, the evergreen forest of the main Andean rivers, the Orinoquian savannas, and the xerophitic forest at the Caribbean coast (Rangel-Ch, 2004; 2012; Angarita-Sierra, 2009; 2014). This species has a high tolerance to disturbed or transformed habitats s such as oil palm plantations and annual crops.

Recently, aspects of its hemipenial morphology, taxonomy, phylogeny and geographic variation have been studied (McCranie and Wilson, 1995; Ingrasci, 2011; Angarita-Sierra, 2009; 2014). Nevertheless, some of its basic biological features such as reproductive cycle, diet, antipredator behavior and ecological interactions remain unknown. Antipredator displays such as crouching, elevated body loops, and dorsoventral neck compression (Savage, 2002; Köhler, 2008) have been reported for only a few species of the genus [*N. celata* (McCranie and Wilson, 1995), *N. hudsoni* (Parker, 1940), *N. maculate* (Peters, 1861), *N. psephota* (Cope, 1876), and *N. sebae* (Duméril, Bribon, and Duméril, 1854)]. Therefore, in the present chapter the antipredator behavior *N. atrata* was assessed exploring the effects of ontogeny and sex.

6.3.3 Methods

As part of an ongoing study of population dynamics, antipredator behavior of individuals from a population of *N. atrata* was examined based on simulations of predator attacks in natural environment. Fieldwork was carried out in oil palm plantation of PALMASOL S.A. at Vereda La Castañeda, municipality of San Martin, department of Meta-Colombia (3°31´46, 6” N; 73°32´15, 3” W). The plantation is located on the piedmont forests of the eastern slopes of the Cordillera Oriental, as well as on high savanna plateaus. Annual rainfall at the site is 3,070 mm. Individuals of *N. atrata* were found by systematic search between August 2014 and January 2015. Searches were conducted by removing piles of palm leaves from 8:00h to 17:30h. Immediately after each encounter, individuals were put in cloth bags to be measured and marked. A session of predator attack simulations was performed the next morning before releasing the snakes at the same place where they were caught. The simulation procedure followed Tozetti *et al.* (2009) and consisted in eight repeated movements of the researcher’s open hand towards the snake’s head at a constant speed. The time to perform the eight approaches was not longer than 10 seconds. Exhibited antipredator displays were classified according to Arnold and Bennett (1984) and Greene (1988). A multidimensional scaling test was performed to assess if a behavioral pattern is associated with the stage of maturity or sex (see Parker & Plummer, 1987; Dorcas and Wilson, 2006). The measure used in multidimensional scaling test was “Kruskal´s stress” (S) (Fox *et al.,* 2014), which is an average of the deviations between the end and the initial spatial distances normalized to take values between 0 and 1. Values near 1 indicate the worst fit, and values near 0 indicate the best fit. However, values between 0.025-0.05 are considered good values, < 0.025 are excellent, and values equal 0 are perfect (Guisande *et al.,* 2014). This test was carried out using the software Rwizard version 2.3 (Guisande *et al.,* 2014) and the MDS function of the vegan package (Oksanen *et al.,* 2013). The function “scatterplot” of the car package was used to generate the biplot graphic (Fox *et al.,* 2014).

6.3.4 Results

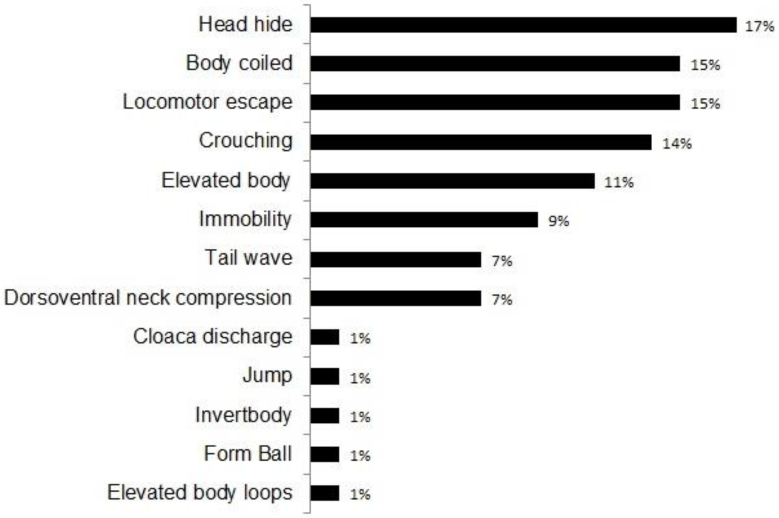

Figure 19. Frequencies of antipredator displays in *Ninia atrata*.

A total of 20 specimens of *N. atrata* were observed during the stimulatory sessions (12 females and 8 males) including five newborns, five juveniles and ten adults. As a result, 13 antipredator displays were recorded, as well as three combined antipredator displays and one social response (Figure 19). Among the 13 behaviors observed, the most frequent displays were head hide (17%), body coiled (15%), locomotor scape (15%) and crouching (14%). On the contrary, the least frequent displays were cloacal discharge (1%), jump (1%), invertbody (1%), ball position (1%), and elevate body loops (1%) Figure 19. The social response was recorded after putting together nine specimens of *N. atrata*, which were found under the same piles of palm leaves (one female and eight male), in the cloth bag. After 24 hours of cohabitation within limited space, the specimens organized themself into a spherical form (ball position) (Figure 20-A). Snakes maintained the spherical formation with heads in the center of the ball and tails on the outside during at least 12 to 15 minutes. The first combined antipredator display resulted from the merge of elevation body, dorsoventral neck compression and invertbody behavior originating a remarkable defensive display (Figure 20-G). The second behavior merges head hide and crouching behavior (Figure 20F and I) and the third combined behavior merges elevate body and dorsoventral neck compression resulting in a body posture similar to the observed in the King Cobra

[*Ophiophagus hannah* (Cantor, 1836)] (Figure 20-H). One juvenile showed ball position with head exposed (Figure 20-O). This was a combined antipredator display resulted from the merge of ball position and head exposed displays. During fieldwork, snakes were handled carefully; however, manipulations frequently stress snakes. As a consequence of this stress, most of the specimens (70 of the 89 specimens observed during the sampling period) exhibited some of the 13 antipredator displays registered.

6.3.5 Discussion

Antipredator behaviors observed in *N. atrata* follow a general pattern of hierarchical decision making (see Roth and Johnson, 2004): (1) if a predator stimuli is detected, the reaction is to retreat (escape behavior), (2) if the threatening stimulus persists, the reaction is to employ passive deterrents (head hide, body coiled, crouching, immobility, tail wave, elevated body loops, ball position), and (3) if the threat further escalates, the reaction is to engage in aggressive defense (dorsoventral neck compression, invertbody, elevated body, jump, cloaca discharge). Similar hierarchical responses have been reported in a wide variety of terrestrial snakes from temperate latitudes (Greene, 1979; Gibbons and Dorcas, 2002; Roth & Johnson, 2004). However, comparisons with South American snakes are not possible because this behavioral feature is unknown for related taxa.

Figure 20. Repertoire of antipredator displays in *Ninia atrata*. A – Social response; B – Tail wave; C – Elevated body loops; D –Ball position; E – Body coiled; F – Crouching; G – Combined antipredator display (elevated body, dorsoventral neck compression and invertbody behavior); H – Dorsoventral neck compression; I – Head hide; J – Immobility; K – Elevated body, Tail; L – Elevated body, Head; M – Invert body; N – Locomotor escape; O – Ball position with head exposed.

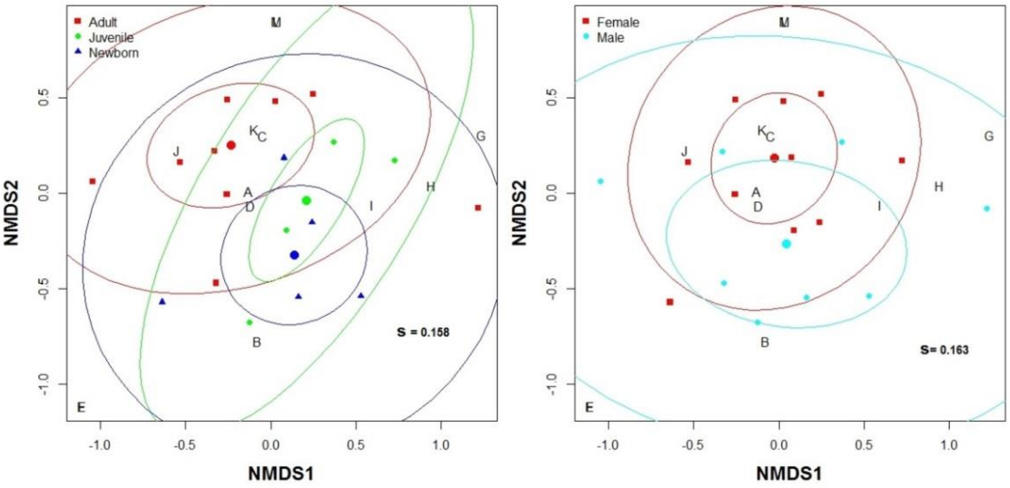

Figure 21. Multidimensional scaling test of antipredator displays in *Ninia atrata*: Inner ellipse represents 0.5 of significance; outer ellipse represents 0.95 of significance. Left: Stage of maturity. Right: Gender comparison Defensive plays: A – Head hide; B – Immobility; C – Crouching; D – Locomotor scape; E – Elevate body; F – Ball position; G – Invertbody; H – Dorsoventral neck compression; I – Elevated body; J – Tail wave; K – Body coiled; L – Jump; M – Cloacal discharge.

On other hand, the multidimensional scaling test showed high stress values (S), which means that behavioral patterns evaluated might not be associated with the stage of maturity (S=0.158) or sex (S=0.163) (Figure 21). These results are not in agreement with the conclusions of other studies that have demonstrated that differences in sex or stage of maturity affect individual responses to predation risk (Clutton-Brock, 1991; Magurran & Nowak, 1991; Krause *et al.,* 1998; Madsen and Shine, 2000; Shine et al., 2000; Roth and Johnson, 2004). Perhaps antipredator response of *N. atrata* is more correlated to the phylogeny (Martins, 1996; Martins *et al.,* 2008) or microhabitat use (Greene, 1979; Senter, 1999; Martins *et al.,* 2008; Tozetti *et al.,* 2009) rather than the intrinsically biological features such as body size, sex, or locomotor ability (Lima, 1998). The most frequent displays such as head hide, body coiled, locomotor scape, and crouching have been observed in *N. atrata* as well as a wide variety of terrestrial snakes that conform the Neotropical rainforests communities (Martins et al., 2008). These set of defensive behaviors has been suggested as characteristic of the Neotropical terrestrial species which have a related evolutionary history (Martins, 1996.)

According to the Optimality Theory, the behavioral response of an individual to a predator is influenced by the risk of predation (Ydenberg & Dill, 1986; Lima & Dill, 1990; Cooper & Vitt, 2002; Roth & Johnson, 2004). Hence, the advantage of the defensive tactic comprises a diverse set of defensive displays, in which the snakes usually achieved a horizontal body expansion that maximizes their visible areas in dorsal view. These displays might intimidate a predator approaching from above. The most frequent displays observed (head hide, body coiled, locomotor scape, and crouching) are often associated with defense against visually oriented predators (Greene, 1988; Sazima & Martins, 1990; Oliveira *et al.,* 2001; Oliveira, 2005; Martins *et al.,* 2008; Tozetti *et al.,* 2009). Also, less frequent displays observed such as ball position, elevated body loops and tail wave have been reported as behaviors that minimize injury to the head during predatory attack in terrestrial snakes (Arnold & Bennett, 1984). All these defensive displays have been categorized as typical in fossorial, semifossorial or terrestrial species (Greene, 1979; Martins *et al.,* 2008) against attacks of predators that approach from above (Arnold & Bennett, 1984; Senter, 1999). Complementary field and laboratory studies are needed to understand the behavioral responses patterns related with body size and sex as well as behavioral convergence between related taxa that inhabit the same biogeographic units. Moreover, more attention should be given to the diverse selective processes caused by the action of different type of predators and environments.

6.3.6 Literature cited

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7. Chapter 2: Snakes in the palms: Snake-human conflict assessment at oil palm plantations (Meta, Colombia)

7.1 Abstract

Sources of snake mortality have been explored broadly on temperate ecosystems, but neglected on tropical ecosystems. Despite the disparity between the number of researches on temperate and tropical zones, a worldwide consensus states that, currently, snake populations presented a gradual decline due multi-faceted factors. For many snake populations the intentional snake killing by humans represent a significant source of mortality. However, the traditional research approaches on this particular source of mortality have followed a “snake biological perspective” which leaves aside the “human perspective” on human-snake conflict. Herein, I explored the patterns of intentional snake killing in a snake assemblage that inhabits oil palm plantations from Orinoquia region of Colombia, employing a “human perspective” as a research approach. Thus, I used information of 167 field workers surveyed as well as the records of 667 snakes obtained during the sampling period 2014-2017 to test the hypothesis that the snake mortality risk is associated with task developed by field workers. As a result, it was clear that the pattern of intentional snake killing on agricultural landscape can be predicted from tasks developed by field workers. However, this pattern is affected by underlying factors such as the way in which field workers experienced fear and by demographic factors that characterize the workforce, rather than by seasonality or climatic variability on snake abundances or richness. Particularly, among the demographic factors assessed, gender and education level seem to be the most significant determinants on the field workers proclivity to kill snakes. Finally, it is necessary to develop management farming strategies that increasing the women proportion by field tasks because this will contribute to decrease the malicious attitudes toward snakes, as well as promotes a sustainable and wildlife friendly agriculture.

Key words: Snakebite, mortality, fear, agricultural landscape, monoculture, threat, conservation.

7.2 Introduction

Oil palm plantations have had an accelerated expansion in the South American tropical countries, supported by increasing demand of palm oil and its by-products such as olein and palm stearines by cosmetic and food industries (Pardo, et al., 2015). More than one million of hectares have been sown in South America of which five hundred thousand in Colombia (FEDEPALMA, 2014). The Colombian Orinoquia region produces the greatest amount of oil palm in the country, mainly focused in the department of Meta (Pardo, et al., 2015). These monocultures have concentrated a huge amount of field workers from several territories of the country, as well as a great abundance and diversity of snakes.

According with Lynch (2012), more than 35 species of snakes inhabit oil palm plantations in Colombia, being the most common species Hallowell's ground snake (*Atractus univittatus),* Fer-de-Lance *(Bothrops asper),* common lancehead *(Bothrops atrox),* brown rainbow boa *(Epicrates maurus),* banded cat-eyed snake *(Leptodeira annulata),* Shaw's dark ground snake *(Erythrolamprus melanotus),* coffee snake *(Ninia atrata),* forest flame snake *(Oxyrhopus petolarius),* Neuwied's false boa *(Pseudoboa neuwiedii),* and black-headed snake *(Tantilla melanocephala*). The snake encounter-rate estimated in the oil palm plantations from Colombia Orinoquia region was 6 snakes per hour, reaching 36 snakes capture per day in a single sampling occasion. This remarkable snake abundance at a Neotropical agricultural landscape provides an appropriate scenario to study patterns of the human-snake conflict.

In Colombia, snakes are part of the idiosyncrasy and collective imaginary of the country. They are often seen as bad omens, problems, debts or creditors (Montaña, 1987). However, aversion and fear for snakes is not unfounded. Colombia ranks third in number of snakebites per year (~4,750), and sixth in snakebite incidents per 100,000 inhabitants (~9.1) among South American countries (INS, 2016, Chippaux, 2017). Besides, since snakebites is part of the neglected diseases by the national health authorities (Lynch, et al., 2014), for many peasants a snakebite represents a death sentence. As a consequence of this cultural tradition and the potential health hazard represented by these reptiles, most Colombians consider all snakes a dangerous threat and agree with the common saying that states: "the only good snake is a dead snake” (Shine & Bonnet, 2000; Campbell & Lamar, 2004, Moore, 2012; Whitaker & Shine, 2000).

Generally, the human-snake conflict focuses on rural or sub-urban areas, since a high proportion of people living in urban areas have never seen a snake in their daily lives (Dood, 1987). Therefore, intentional snake killing is carried out by peasants or field workers (Whitaker and Shine, 2000). Several studies have suggested that intentional snake killing induces their population decline, as well as top-down effects on the ecosystems (Dood, 1987, Todd, et al, 2010, Brown, et al, 2013, Das, 2013). In particular, Bonnet et al (1999) developed a comprehensive study on patterns of anthropogenic mortality on snake populations at temperate latitudes, concluding that a prime determinant of snake mortality risk is movement; particularly, the dispersal from the usual home range due to reproductive, development or foraging requirements. However, all these studies have explored the direct snake killing from a “snake biological perspective”, without regarding the dynamic of human activities as drivers of the snake vulnerability during human-snake conflict. Hence, little attention has been devoted to understand the patterns of the human-snake conflict that provoke the intentional snake killing from a “human perspective”.

In the present chapter I studied the patterns of intentional snake killing in a snake assemblage that inhabits oil palm plantations in the Orinoquia region of Colombia. In order to asses this anthropogenic source of snake mortality the following hypothesis was proposed: given that human-snake conflict comes out from encounter between people and snakes, snake mortality risk is associated with tasks developed by field workers. Risk is understood here as the snake´s exposure to the chance of being injured or killed. I based this hypothesis on my experience working with snakes at agricultural landscapes, and from published literature suggesting that some types of human activities and the snakes’ activity within their usual home range promotes a high encounter rate (Dood, 1987, Bonnet, et al., 1999, Shine & Bonnet, 2000, Whitaker & Shine 2000, Zhou & Jiang, 2004, Das, 2013, Lynch, 2012, 2015). I also contrast the intentional snake killing rate estimated herein with the estimated by Lynch (2012) and Lynch et al (2014) for lowlands snake assemblages in Colombia, considering factors such as seasonality, motivation for intentional snake killing, as well as socio-demographic aspects of the workforce at oil palm plantations.

7.3 Methods

7.3.1 Study area and data collection

Fieldwork was carried out in oil palm plantation of PALMASOL S.A. at vereda La Castañeda, municipality of San Martin, department of Meta-Colombia (3°31´46, 6” N; 73°32´15, 3” W), in four production batches of palms *Elaeis guineensis* (Jacq 1897) that are between 32 and 36 years old. The plantation is located on the piedmont forests of the eastern slopes of the Cordillera Oriental, and on high savanna plateaus (Figure 1).

Weather is characterized by monomodal climate (rainy season from April to November, and dry season from December to March) with annual rainfall of 3,070 mm and high temperatures (> 26°C) year-round. The strongest El Niño–Southern Oscillation phenomenon (ENSO) of the last 20 years took place during the study period (IDEAM, 2016). This climatic event had a deep impact on the high savanna plateaus of the Llanos Orientales of Colombia causing high temperatures and low moisture during dry season, and a deficiency of rainfalls during rainy season. Therefore, climatic variability was categorized in good years, representing periods without ENSO effects (from Aug 2014 to December 2015), and bad years (from Jan 2016 to June 2017), representing periods under ENSO effects

Snake’s sampling was conducted monthly from 7:30 to 17:30 during three sampling days by five researchers, investing 1189 hours of sampling effort per researcher on period 2014-2017. All snake individuals were found by systematic removal piles of palm leaves and the epiphytic mattress from the base of the palms.

Records of snake mortality as result from human activities were obtained in two ways. First, a total of 167 structured surveys were made to field workers at oil palm plantation of PALMASOL S.A during the period 2016-2017, following the procedure described by Whitaker and Shine (2000). The surveyed peasants and field workers were asked about basic socio-economic data (sex, age, education level, and place of origin), work performed, and effort per day of the work performed in the annual production cycle. Education level were categorized as low (primary education), mid (junior high school, or high school) and High (university or vocational school) Likewise, field workers were asked: How many snakes they have seen in the current and last week? Of the snakes sighted, How many have you killed?, and Why? (Supplement 1). Additionally, in order to determine whether peasants were able to distinguish between venomous and non-venomous species, an illustrative sheet with pictures of five snake species that inhabit in oil palm plantation was shown (*Ninia atrata, Bothrops atrox, Oxyrhopus petolarius, Micrurus dumerilii, Trilepida macrolepis*), and then, they were asked: Which of these snakes they think is venomous? (Supplement 2). The answer was categorized as “Good” when the surveyed chose both venomous snakes shown in the illustrative sheet, “Partial” when the surveyed chose only one venomous snake, one venomous and one non-venomous snake, or both venomous snakes and one non-venomous snake, and “Bad” when the surveyed chose only non-venomous snakes, one venomous snake and two or more non-venomous snakes, or when the surveyed openly states that she/he didn’t know.

Second, supported by the Health, Safety, Environment and Quality (HSEQ) manager office of the oil palm plantation of PALMASOL S.A, barrels with formalin (25%) were made available to field workers to deposit the snakes killed by them throughout the period 2014-2017. All these specimens were deposited in the reptile collection of the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional de Colombia. Additionally, when a field worker killed or sighted a snake during their daily tasks an encounter form was completed with the HSEQ manager’s support. Finally, information about the number of fieldworkers at the plantation per year, daily tasks performed per worker, and numbers of snakebites incidents per year were obtained from HSEQ database of PALMASOL S.A. Given the wide variety of tasks developed by field workers, these were classified as agricultural management and technical tasks, animal management and pest control, engine driving, fruit piking, multitask, pollination, and pruning (Supplement 3).

7.3.1.1Statistical analysis

In order to test the predictions derived from the "snakes' mortality risk associated to task" hypothesis, I employed a hypothesis-testing strategy through of contrasts of homogeneity of variables, as follow. If we assume that the mortality risk for a snake depends on the task developed by a field worker, we can expect: First, intentional snake killing rate, as well as snake encounter rate per field worker does not exhibit a seasonal variability, despite the fact that tropical snakes' assemblages having a remarkable change on abundance and richness between seasons (Martins & Oliveira, 1998, Madsen & Shine, 2000). Hence, a Chi-square (χ^2) tests with Yates correction and Kruskal-Wallis tests were performed having as null hypothesis that the encounter and snake killing rate don't have seasonal changes. Likewise, a one way ANOVA and an ANCOVA were employed to evaluate the seasonality and climatic variability of the snake assemblage that inhabit oil palm plantations during the sampling period.

Second, we can expect that the encounter and intentional killing rate be highest at field tasks that cover long distances or generate high microhabitat disturbances. Therefore, a G-test and a Chi-square (χ^2) test were performed, considering as null hypothesis that the ratio of expected frequencies is the same in all the tasks assessed.

Third, because tasks at oil palm plantations occur mainly during daytime, we can expect that diurnal snakes rather than nocturnal snakes present a highest mortality risk by intentional snake killing. Thus, a G-test and Chi-square (χ^2) test were performed, considering as null hypothesis that the ratio of expected frequencies is the same in diurnal and nocturnal snakes. Species such as

Bothrops atrox or *Tantilla melanocephala* that exhibit a twilight activity were considered as nocturnal.

Fourth, due to the division of labors and traditional social organization in Colombia's countryside (Hudson, 2010), we can expect differences on the intentional snake killing between sexes or age rank within field workers. Therefore, a G-test and Chi-square (χ^2) test were performed, considering as null hypothesis that the ratio of expected frequencies is the same in all demographic factors assessed. The association degree between demographic factors was assessed throughout Cramer's V coefficient and Contingency coefficient (Guisande-Gonzáles, et al., 2014).

Fifth, given that education has been considered as an important factor on human attitudes toward wildlife (Burghardt, et al., 2009, Balakrishnan, 2010), we can expect differences on the intentional snake killing rate between the field workers´ education levels. Thus, a G-test and a Chi-square (χ^2) test were performed, considering as null hypothesis that the ratio of expected frequencies is the same in all field workers´ education levels.

Finally, to contrast the intentional snake killing rate observed with the one estimated by Lynch (2012) and Lynch et al (2014), a Wilcoxon test was performed, considering as null hypothesis the killing rate scores reported by these authors against the alternative hypothesis that the median score observed is not equal. Afterwards, I compared my results with the biological cost caused by intentional snake killing based on estimation of Lynch et al (2014) on rural areas from Orinoquia region. Thus, a Wilcoxon test was carried out based on the assumption that one member of a farmer family ("censual home") kills snakes when she/he is developing similar farm activities to those observed at oil palm plantation (e.g. pruning, harvesting, soil plowing, etc.). The database of the Colombian National Administrative Department of Statistics (DANE) was consulted to obtain number of "censual home" in the Colombian Orinoquia region. According with this institution a "censual home" is defined as a person or group of people, relatives or not, who live (sleep) in the same home and share, generally, their meals (DANE, 2008). All statistical analyses were done employing the software Rwizard 2.3 (Guisande–Gonzáles, et al., 2014) and using the R packages "car" (Fox & Weiberg, 2011) and "stats" (R Core team, 2012).

7.4 Results

The workforce at oil palm plantation under study was composed by a monthly average of 77.5 ±26.01 field workers from diverse origins, ages and education levels. Workers come from 24 of the 33 departments of Colombia, being Meta (48.5%) and Antioquia (5.9%) the main sources of field workers. Men in ages that range from 18 to 64 years old, and particularly between 18 to 39 years old, are the main workforce. Women represented 18% of the total workforce with ages that range from 18 to 49 years old, being women between 18 to 24 and 30 to 34 year old the main women workforce (Figure 22A). Education levels of the workforce ranges from universities studies to illiteracy, being mostly grouped at mid (58.1%) or low (23.4%) education levels. However, women showed significantly higher education level than men (χ^2= 29.6, P< 0.0001, n= 167) having complete studies of high school, vocational school or university.

Between field worker´s gender, women exhibited a low tendency to kill snakes, showing a significant difference with respect to men (χ^2= 4.98, P= 0.025, n= 96). In contrast, snake kill tendency within men did not show significant differences (Figure 22B). Likewise, women vs. men reactions toward a snake encounter showed remarkable differences suggesting that gender is among the most important demographic influences on the intentional snake killing (Table 5). Particularly, women (86.6%, n=15) displayed a higher significant frequency of retreat or passive deterrent behaviors than men (53.9%, n=89), whom in contrast, acted actively to deal with the potential hazard represented in these reptiles, displaying aggressive behaviors such as attacking, or moving towards the snakes. Similarly, education level within the field workers who have seen snakes and killed them showed to be an important demographic influence on the attitude toward snakes. In particular, field workers with mid to low education levels had a major proclivity to kill snakes (χ^2= 18.541, P< 0.0001), being this attitude independent of the field workers gender (Cramer's V= 0.11, Contingency coefficient= 0.11).

Table 5. Reactions toward snake encounter by gender. χ^2 = Chi-square test. (*) Other reactions toward snake encounter such as: call a friend, scream, and cry.

Reaction	Women %	Men %	Comparisons	χ^2	P	n
He/She moved towards the snake	0	12.3	**Between genders=**	31.2	**<0.0001**	104
He/She attacked the snake	6.6	31.5				
He/She ignored the snake	20	23.6	**Within women=**	14.6	**0.002**	15
He/She ran away	66.6	9.0				
He/She stays still	6.6	21.3	**Within Men=**	26.1	**<0.0001**	89
Other*	0	4.5				

However, contrary to expectations, more than half of the field workers that sighted snakes did not kill them (65%, n=96), showing significant difference between snakes seen and killed, and snakes seen but not killed per field worker (χ^2= 6.0, P= 0.014, n= 96). Moreover, the field task was not a significant factor on the decision to kill the snakes seen (χ^2= 9.07, P= 0.17, n= 60). The main motivations to kill (or not kill) snakes expressed by 102 field workers surveyed were: caution (40%), self-defense (23%) and fear (22%). These motivations were significant (χ^2= 62.94, P< 0.0001, n= 102), and independent of age rank (Table 6).

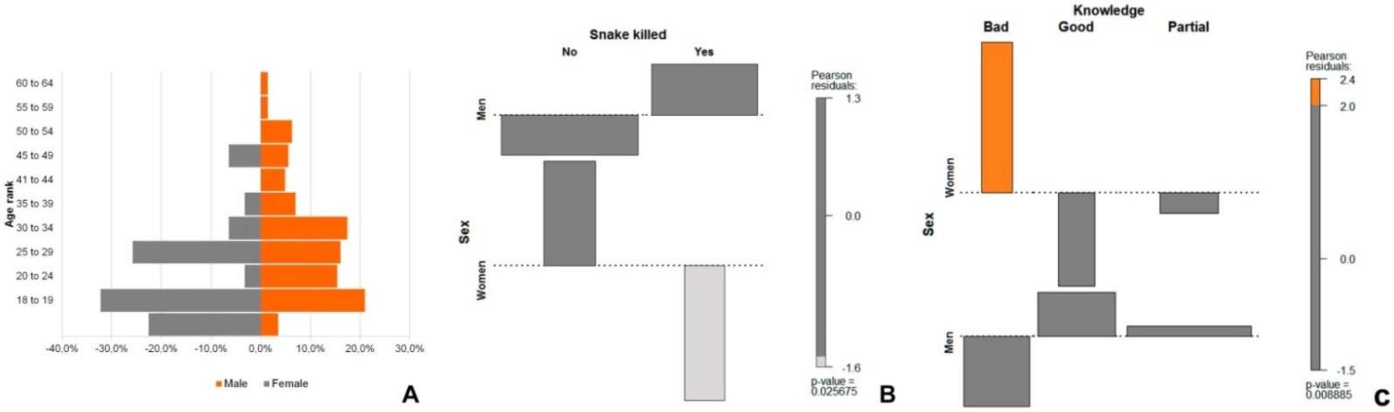

Figure 22. Genders proportion, intentional snake killing tendency within genders, and knowledge of snakes of the workforce at oil palm plantation. A) Demographic pyramid of the workforce surveyed. B) Chi-square test that show the intentional snake killing tendency between genders of the workforce. C) Chi-square test that show the knowledge of venomous and non-venomous snakes between genders of the workforce.

Remarkable snake diversity was found during sampling period. Taxonomic richness was composed by sixteen species, four families, and fourteen genera. Of 664 snakes detected during the period 2014-2017, 75% (n=16) were nocturnal species being the most common *Ninia atrata, Bothrops atrox and Atractus univittatus*. *Bothrops atrox* was the unique venomous snake detected throughout study. A total of 224 snakes were sighted by surveyed field workers, of which 50 snakes were intentionally killed during the period 2016-2017. The killed snakes represented 62.5% (n=16) of the species richness inhabiting the oil palm plantation. Also, this source of mortality acted in the same way in all population-levels of each species (male, females, neonates, juveniles, adults) indicating that it has not selective behavior.

Table 6. Motivations to kill snakes expressed by field workers at oil palm plantation of PALMASOL S.A

Motivation	Percentage %	Pearson's χ^2 test	P	Cramer's V	Contingency Coefficient
Caution	40,20	7.02	0.22	0.18	0.19
Self-defense	22,55				
Fear	21,57				
Defense of Others	8,82				
No reason	4,90				
Magic-religious beliefs	1,96				

Contrary to predictions, nocturnal rather than diurnal snakes showed significantly higher killing rate (χ^2= 10.45, P= 0.001, n=34). The most frequent snakes killed and deposited in the barrels with formalin were *Bothrops atrox*, followed by *Atractus elaps*, *Erythrolamprus bizona* and *Leptodeira annulata* (Table 7

Table 1). Also, worm lizards were frequently killed and deposited in the barrels with formalin (*Amphisbaena alba* and *Amphisbaena fuliginosa*). These results agree with the high proportion of field workers (77%, n= 162) who were unable to distinguish suitably between venomous and non-venomous snakes. Consequently, worm lizards and harmless snakes such as *Atractus elaps*, *Erythrolamprus bizona* and *Leptodeira annulata* frequently were killed due to its similarity with venomous snakes (e.g. *Bothrops atrox or Micrurrus dumerilli*) despite of their low relative abundance (Table 7).

In fact, more than half of the farmhand surveyed (63%, n=162) presented a partial knowledge about venomous and non-venomous snakes, being noteworthy the number of field workers that choose only one venomous snake, or one venomous and one non-venomous snake as a potential hazard (χ^2= 30.47, P< 0.0001, n=162). Particularly, men had higher knowledge about venomous and non-venomous snakes than women (χ^2= 9.5, P< 0.01, n=104), being significant the difference between men and women that were unable to distinguish between venomous and non-venomous snakes (Figure 22C).

On the other hand, significant differences on the snake abundance between rainy and dry season were observed (Figure 23), as well as between climatic years ($\text{ANCOVA}_{\text{season}}$, P= 0.002, n= 32; $\text{ANOVA}_{\text{climatic years}}$, P< 0.0001, n= 32). Snakes are more abundant during rainy seasons and good climatic years than during dry season or bad climatic years. In contrast, the encounter and snakes kill rates does not show significant differences between seasons, being snakes more abundant during rainy seasons and good climatic years than during dry season or bad climatic years. In contrast, the encounter and snakes kill rates does not show significant differences between seasons ($\chi^2_{\text{snake killing rate}}$= 2.88, P= 0.089, n=167; $H_{\text{encounter rate}}$= 2.70, P= 0.10, n=167). Through their daily tasks, the mean snake encounter rate was 1.97 snakes per field worker/week (Table 8). The field task that provoke the highest mean encounter rate per fieldworker was engine driving ($\bar{x}$= 2.13), followed by fruit picking ($\bar{x}$= 1.67), and pruning ($\bar{x}$= 1.60).

Likewise, the field task that exhibited the highest proportion of snakes sighted and killed were animal management and pest control (50%) and engine driving (41%). Consequently, among the field workers who saw snakes (n= 97), both encounter and snake killed rates showed significant differences between the field tasks assessed, indicating that engine driving, fruit piking and pruning promotes snake sightings, and, engine driving and pruning provokes the highest number of snakes killed ($\chi^2_{\text{encounter rate}}= 59.99$, $P< 0.001$, n= 6; $\chi^2_{\text{snakes killed}} = 21.68$, $P= 0.001$, n= 6). It was also observed that as the proportion of women in field tasks increase, the number of snakes sighted and killed decreases (Figure 24), showing an inverse relationship between women proportion by field tasks and the proportion of snakes sighted and killed ($R^2= 0.27$, $P= 0.007$, n= 7).

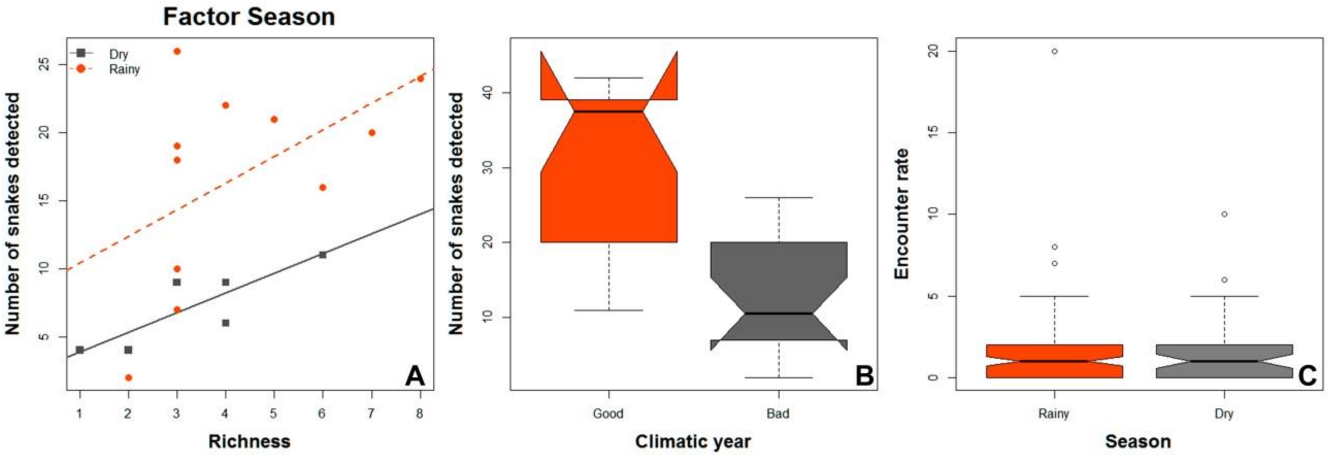

Figure 23. Seasonally snakes variation and field worker´s encounter rate with snakes. A) ANCOVA of season variability of snakes detected through period 2016-2017 using as covariable snake richness. B) ANOVA of number of snakes detected through climatic years (without ENSO effect period 2014-2015, under ENSO effect 2016-2017). C) Field workers´ snake encounter rate between seasons during the period 2016-2017.

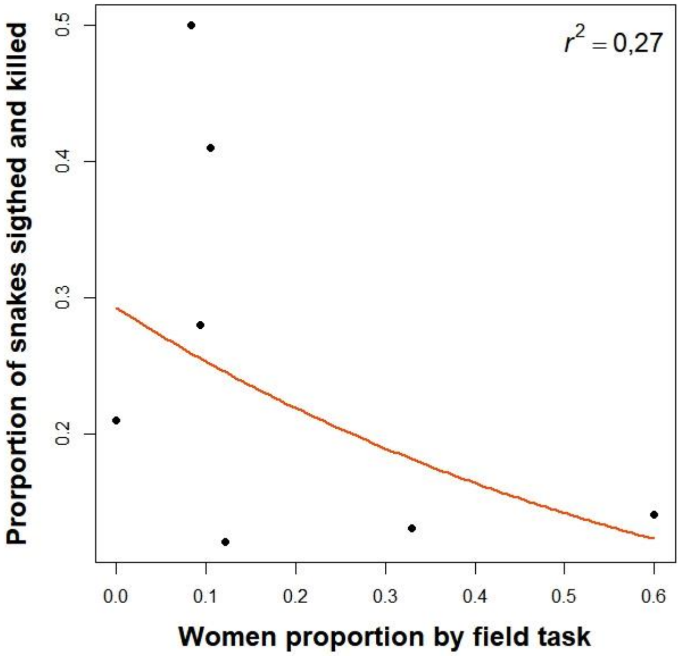

Figure 24. Relationship between women proportion by field tasks and the proportion of snakes sighted and killed. Regression formula: $y = -1.23e^{-1.45}$. Normality test (Kolmogorov-Smirnov): D= 0.22, P= 0.40; Durbin-Watson autocorrelation test: DW= 2.33, P= 0.74; Breusch-Pagan homoscedasticity test: BP= 1.79, P= 0.28.

Table 7. Taxonomic diversity of the snake assemblage that inhabit oil palm plantations of the company PALMASOL S.A. n= number of individuals observed during sampling period.

Family	Genus	Species	Activity	n	Relative abundance (%)	Snakes deposited in formalin barrels
Boidae	Boa	*Boa constrictor*	Diurnal	1	0.15	0
Colubridae	Atractus	*Atractus elaps*	Nocturnal	8	1.20	3
		Atractus major	Nocturnal	1	0.15	0
		Atractus univittatus	Nocturnal	24	3.61	2
	Chironius	*Chironius carinatus*	Diurnal	4	0.60	2
	Erythrolamprus	*Erythrolamprus bizona*	Diurnal	12	1.81	4
	Imantodes	*Imantodes cenchoa*	Nocturnal	1	0.15	0
	Leptodeira	*Leptodeira annulata*	Nocturnal	9	1.36	3
	Leptophis	*Leptophis ahaetulla*	Diurnal	1	0.15	1
	Ninia	*Ninia atrata*	Nocturnal	443	66.72	2
	Oxyrhopus	*Oxyrhopus petolarius*	Nocturnal	6	0.90	0
	Pseudoboa	*Pseudoboa neuwiedii*	Nocturnal	3	0.45	1
	Siphlophis	*Siphlophis compressus**	Nocturnal	1	0.15	1
	Tantilla	*Tantilla melanocephala*	Nocturnal	20	3.01	2
Typhlopidae	Amerotyphlops	*Amerotyphlops reticulatus*	Unknown	7	1.05	0
Viperidae	Bothrops	*Bothrops atrox*	Nocturnal	123	18.52	13
			Total	**664**	**100**	**34**

Finally, 83% of the snake killing rates estimated by Lynch (2012) and Lynch et al (2014) exhibited significant differences with the weekly mean killing rate estimated in the present study, as well as seasonal killing rates observed throughout period 2014-2017 (Table 8). These authors overestimate or underrate the outlier values observed in the present study (e.g. snake killing rate outlier values= 13 and 17). Nonetheless, a weekly median killing rate that ranges from three to four snakes killed by field workers suggests being the consensus value between killing rate estimated herein and the estimated by Lynch (2012) and Lynch et al (2014). Likewise, the biological cost derived from intentional snake killing by field workers in Orinioquía region estimated by these authors is significantly higher than the one observed in the present study (Table 9), and overestimate (W= 2277,P= 0.001). Particularly, my results showed that the median rank of weekly snakes killed workers (1000 to 5000 snakes killed/week) is ten times lower than the rank estimated by Lynch et al (2014) the Colombian Orinoquia lowlands snake assemblages (Figure 25).

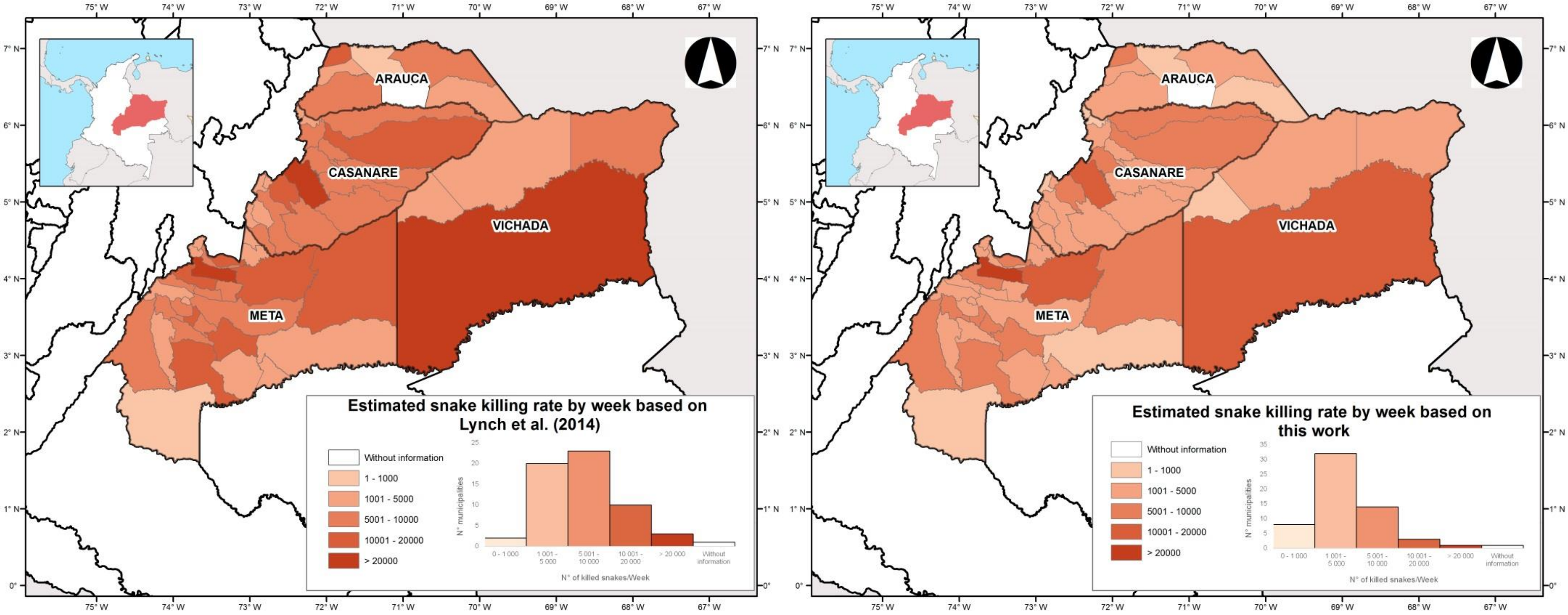

Figure 25. Snake killing rates comparison among municipalities from Orinoquia region. (Left) Estimated snake killing rate by week based on Lynch et al. (2014). (Right) Estimated snake killing rate by week based on this work.

Table 8. Summary of snakes seen and killed by fieldworkers during period 2016-2017 at oil palm plantation PALMASOL S.A. Values in brackets represent mean encounter rate per field task weekly.

Field task	Mean working hours	Number of employees	Field worker´s gender proportion	Snakes seen per employee	Proportion of snakes seen and killed
Agricultural management and technical tasks	8.38	33	♀= 33%, ♂= 67%	N= 31 (x̄= 1.49)	13%
Animal management and pest control	8.30	12	♀= 8.3%, ♂= 91.7%	N= 6 (x̄= 1.37)	50%
Engine driving	8.34	19	♀= 10.5%, ♂= 89.5%	N= 41 (x̄= 2.13)	41%
Fruit piking	8.30	33	♀= 12.1, ♂= 87.9%	N= 58 (x̄= 1.67)	12%
Multitask	8.31	32	♀= 9.4%, ♂= 90.6%	N= 29 (x̄= 1.50)	28%
Pollination	8.30	15	♀= 60%, ♂= 40%	N= 14 (x̄= 1.41)	14 %
Pruning	8.30	23	♀= 0%, ♂= 100%	N= 44 (x̄= 1.60)	21%

Table 9. Comparisons between the mean snakes killing rate observed in the present study and the snake killing rates estimated by Lynch (2012) and Lynch et al., (2014) for lowlands snakes´ assemblages from Colombia throughout a Wilcoxon test. (*) denotes weekly mean snake killing rate reported by Lynch (2012). (†) denotes weekly snake killing rate reported by Lynch et al (2014). SD= Standard deviation. m=mode, n= Total number of snake intentional killed by field workers during 2014-2017.

Weekly snake killing rate (Lynch 2012, Lynch et al., 2014)	Wilcoxon test value (Weekly)	P	Wilcoxon test value (Dry season)	P	Wilcoxon test value (Rainy season)	P	Weekly Snake killing rate observed (2014-2017)
9.38*	18	<0.001	0	<0.01	11	<0.01	x̄= 4.16, SD= ±3.44 m= 1 n=100 (1—17)
21	0	<0.0001	0	<0.01	0	<0.001	
17	1	<0.0001	0	<0.01	1	<0.01	
7†	25	<0.001	0	<0.01	15	0.01	
3	186	0.12	33	0.28	68	0.33	
2	207	<0.001	32	0.042	79	0.02	

7.5 Discussion

The main result from this study is that the patterns of intentional snake killing on agricultural landscape can be predicted well from the simple assumption that snake mortality risk is associated with task developed by field worker. Both engine driving and pruning are tasks that provoke the highest intentional killing rates because they employ machines to plow soil, to remove undergrowth, and to carry palm fruit long distances to the processing plant. This agrees with the prediction that field tasks that cover long distances or generate high microhabitat disturbance also provoke highest intentional snake killing rate.

Likewise, as predicted, seasonality or climatic variability on snake abundance or richness was not significant factors that influenced the encounter and snake killing rate. This fact can be explained because, first, the tasks carried out by field workers at oil palm plantation were constant and with similar effort throughout dry and rainy seasons. And second, give that snake assemblage that inhabits oil palm plantations are mainly composed of nocturnal snakes (Lynch, 2012), the changes on snake activity patterns, abundance and richness mediated by seasonality (e.g., foraging or mating) don’t have a significant effect on the snake encounter rate because most of field worker´s tasks are carries out during daytime.

Despite the fact intentional snake killing rate can be predicted well from the tasks developed by field workers, this factor did not proved to be the only cause that contributes to the explanation of the snake killing pattern. Indeed, this pattern showed to be affected by underlying factors such as the way in which field workers experience fear, as well as by demographic features that characterize the workforce.

Fear, as an evolutionary mechanism of defense emerges from the interaction between ecological events and human behavior (Öhman & Mineka, 2001). Even though several ecological events could elicit fear in people, some stimuli, more than other, provoke intense fears. Snakes are animals that lead the lists of common phobias and intense fears (APA, 1994). Therefore, it was expected that caution, self-defense and fear were the main motivations expressed by field workers for killing snakes. Curiously, these motivations also were the main reasons for 65% of field workers that sighted snakes but avoided killing them. This would seem to be a paradoxical result, but in fact, it agrees with avoidance and escape behavior, which is an essential characteristic of fear as an evolutionary defense mechanism (Epstein, 1972). Similar results have been found on different agricultural landscapes. For instance, Whitaker and Shine (2000) found that 50% of the 58 snakes monitored between 1993 and 1995 were killed by peasants, while exploring the mortality sources of some large Australian elapids. When peasants were asked about the motivation for killing snakes the main reasons were fear, family protection and the prevention of a future accident.

The demographic features that characterize the workforce showed to have a deep influence on the intentional snake killing pattern. Firstly, the degree of risk experienced by snakes varies among field worker´s gender. Women tended to express a far stronger repulsion for snakes than men, even though both experienced the same encounter event. Despite the attitudes toward snakes mediated in both genders by fear or caution, men vs. woman differences in attitudes lie in active (kill or confront the threat) or elusive (runaway) behavior displayed.

According with Rakinson (2009) this striking contrast have been found as common and consistent in gender difference in the incidence of ophidiophobia, in which women are four times more likely than men to have fears and phobias for snakes, but not other stimuli (e.g., heights, flying, closed spaces, among other). In contrast, men had a significantly higher utilitarian and dominionistic attitude toward snakes, or wildlife in general, that makes it overcome the potential danger and kill snakes as personal satisfaction from the mastery and control of this reptile (Kellert & Berry, 1987). Consequently, the differences on the intentional snake killing rate between the field tasks assessed are linked with this gender difference, in which, a greater proportion of women in field task would contribute to reduce the proportions of snakes killed. Thus, if greater women proportion by field tasks is promoted throughout strategies of management farming, it could represent a key improvement for a sustainable agriculture and wildlife friendly.

Secondly, education level showed a strong effect on the proclivity to kill snakes. The fact that field workers within mid and low traditional education levels had a strongest tendency to kill snake points out that education, no matters if it does not consider wildlife conservation as particular topic on its formative processes, represented a crucial factor to reduce malicious attitudes towards snakes. Furthermore, the notable difference observed on knowledge about venomous and non-venomous snakes between genders, in which men with lower education levels than women exhibited higher knowledge about snakes, highlights two main conclusions. First, despite the education level reached by the field worker, the gender is a predominant factor that influences how men and woman perceive snakes, and second, that traditional education in Colombia has neglected on teaching wildlife-related education.

Similar results have been found by several researches who have studied attitudes, knowledge and behaviors toward wildlife (e.g., Kellert & Berry, 1987, Ceríaco, 2012), concluding as well as the present study that gender is among the most important demographic factors in determining attitudes about animals in our society. Likewise, education protrudes as a common need in the wildlife conservation strategies, particularly, on snake's conservation planning (USFWS, 1978, Balakrishnan, 2010, Lynch et al 2014). Regrettably, given that both in the lay public and in the management community simply do not like snakes, or they did not consider snakes as a relevant conservation object, the educational strategies focused on the snake conservation have lower support (Seigel & Mullin, 2009).

The results of the present study have direct implications for snake conservation planning. First, the strategies that seek to mitigate the intentional snake killing must consider specific objectives that deal with tasks developed by field workers. Hence, lines of action must be formulated according with the agricultural landscape in which the strategy will be implemented, looking for linking the agroindustry with attitude change towards wildlife inhabiting at its fields. Also, these lines of action must consider the division of labors and traditional social organization by genders.

Second, educational strategies at the snake conservation plans must consider the disparity on attitudes, knowledge and behaviors toward snakes between women and men. Particularly, the educational lines of action must deal with ophidiophobia or intense fears for snakes employing suitable pedagogical methods to induce a positive attitude change on people toward snakes. Historically, in Colombia as well as several countries, direct killing of wildlife has tended to attract more attention from community-based “conservation” organizations than from professional scientists (Bonnet, et al., 1999). Therefore, the effectiveness of the educational strategies has been difficult to track because, generally, mixed pedagogical approaches employed that could produce spurious results (Gutierrez de White & Jacobson, 2010). To ameliorate this scenario, I recommend to prioritize the following wildlife educational methods: modeling and direct contact opportunities (Morgan & Gramann, 1989). I base this suggestion not only in my experince working with peasants and field workers on educational programs, but also from published literature demonstrating that theses methods have been successful combating ophiophobia or intense fears for snakes, and inducing a positive attitude toward snakes (e.g. Festinger, 1957, Geer & Turteltaub, 1967, Tilden, 1977, Morgan & Gramann, 1989, Morgan, 1992).

Education has not only been the keystone strategy to promote positive attitudes on people toward snakes in the agricultural landscape context, or wildlife in general (Morgan, 1992), but also contributes to the prevention of work accidents related to wildlife on agricultural workers. Four snakebite accidents were reported at the oil palm plantation under study during the three years of sampling. All field workers were able to see the snake before the accident happened, but they were unable to prevent the accident because their reaction was to attack the snake that caused the accident. This attitude seems to reflect a general behavior in Colombian field workers. According with the National Health Institute of Colombia, around 82.8% of the field workers that suffered snakebites in the country on 2016 (4704 snakebites accidents on 2016) were able to see the snake before the accident happened.

Thus, the lines of action that deal with snakebite at the snake conservation plans must consider investing significant efforts in teaching preventive behaviors toward snakebites. In particular, these lines of action must enhance the knowledge about venomous and non-venomous snakes among field workers considering its gender differences. This will help to reduce the accidental rate by snakebites, and mitigate the killing rate of harmless snakes due to the fact that most of people cannot distinguish suitably a potentially dangerous snake from one that is not (Whitaker and Shine 2000, Lynch, 2012).

Finally, this study provided an accurate revision of the determinant factors that affect human-snake conflict, with regard to intentional snake killing, helping planners and stakeholders to improve the implementation of national programs for the conservation of snakes in Colombia. In particular, the adjustment of snake killing rate for the Orinoquia region allows a suitable estimation of the biological cost from direct snake killing by humans. This, will aid to prioritize and support the environmental decisions of planners and stakeholders who seek to minimize costs and obtain a better cost-effectiveness ratio (Hily, *et al.,* 2015; Tilsdell & Nantha, 2011). Unfortunately, the insights gained from this study may be difficult to make a generalized result for other agricultural landscapes. This is because the snake killing pattern could have different responses towards diffrerent field task developed, the landscape metrics and the snake assemblage composition. Notwithstanding, this study provides a better understanding of the processes involved in vulnerability of snakes to anthropogenic sources of mortality.

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8. CHAPTER 3: Escaping from certain death: A demographic assessment of the intentional snake killing by humans

8.1 Abstract

Reptile species are declining on a global scale. Ten significant threats to reptile populations are commercial hunting, magic-religious hunting, pollution, intentional killing, road killing, habitat loss, climate change, invasive species, species cascading declines, and infection diseases. Among these, intentional snake killing has been considered a significant source of mortality linked with human activities that threatens the viability of snake populations. However, its real effects on the viability of snake populations have been poorly explored. The high concentration of snakes and human workforce at oil palm plantations offers a unique opportunity to explore the effects of this source of mortality. Herein, I present a demographic assessment of the intentional snake killing on a population of the snake species *Ninia atrata*. To test the expected demographic responses toward four scenarios of intentional snake killing, the Integral Projection Model (IPM) was employed as a demographic approach. The results show that the population structure of the species is mainly composed by neonates, with a significant seasonal variability. Apparent survival rate showed a negative relationship with body mass suggesting that as the snake body mass increases, the chances of survival decreases. Recruitment and fecundity were the main demographic processes driving the population fate, in which heavy weighted snake individuals have the strongest contribution to long-term population size. Finally, the perturbation analyses showed that the intentional snake killing does not represent a significant threat to the viability of the *Ninia atrata* population under study. This suggests that short-lived tropical snake species with a fast life history strategy allocating a high reproductive effort at each of its few reproductive occasions are able to escape from this source of mortality. Consequently, the strategies for snake conservation must consider how fast or slow is the life history strategy of snake species in order to prioritize species, as well as for the implementation of effective lines of actions that maximize cost-effectiveness ratio between financial sacrifice and stated aim.

Key words: Conservation, Threats, Neotropical snakes, integral projection model, vital rates, Demography.

8.2 Introduction

The extinction and vanishing of wildlife due to human activities, is perhaps, one of the most important environmental concern currently. Some of the fundamental questions around this concern involve which are the main sources of wildlife mortality due to human activities, and how these contribute to the extinction risks of their populations. Therefore, remarkable attempts have been made to understand and categorized the anthropogenic mortality effects, as well as to measure the chance that a wild population declines until extinction (Holt, 1987, Shea, 1998, Ceballos, et al., 2017).

Aesthetically pleasing species (essentially birds and large mammals) have been the major focus of conservation actions that predict how and when, do the human activities drive wild populations to extinction (Morris, et al., 1999). Despite snakes being vertebrates that do not have the same popularity and empathy like the giant panda (*Ailuropoda melanoleuca* David, 1869), cheetah (*Acinonyx jubatus* Schreber, 1775) or hawksbill turtle (*Eretmochelys imbricata* Linnaeus, 1766), numbers of snake conservation programs have increased substantially over the last 15 years (Burghardt, et al., 2009, Seigel & Mullin, 2009). These efforts have allowed the categorization of the sources of snake mortality in ten types: commercial hunting, magic-religious hunting, pollution, intentional killing, road killing, habitat loss, climate change, invasive species, cascading declines, and infectious diseases (Bonnet, et al., 1999, Todd, et al., 2010; Bishop, et al., 2016; Lorch, et al., 2016).

Most of these sources of snake mortality have more than one comprehensive study that exposes how these threats are linked with snake populations decline (Reber & Smith, 1996, Bonnet, et al., 1999, Madsen & Shine, 2000, Zhou & Jiang, 2004, Luiselli, et al., 2011, Hyslop, et al., 2012, Brown, et al., 2013, Das, 2013 Guimarães, et al., 2014, Pomara, et al., 2014, Lorch, et al., 2016). Nonetheless, among these sources of mortality, less attention has been paid to the effect of intentional snake killing on wild populations, even though several cases of population decline due to direct snake killing by humans have been documented (Means, 2009; Lyons & Natusch, 2011).

Intentional snake killing in natural populations by humans often occurs at different times and in different places than most natural mortality, and it could be addressed at subsets of the population that differ phenotypically from those that are most vulnerable to natural mortality sources (Shine & Mason, 2004). This source of mortality is influenced by attitudes, knowledge and behaviors toward wildlife, inherent to people that experience the encounter with snakes, as well as the folklore, culture and geographical landscape in which they live (Herzog Jr. & Burghardt, 1988, Morgan & Gramann, 1989, Morgan, 1992). Therefore, direct snake killing by humans is difficult to evaluate due to, first, our poor understanding of the patterns of direct anthropogenic mortality and its relationship with snake life history traits (Bonnet, et al., 1999). Second, it is logistically daunting to quantify anthropogenic mortality rates, given that it is rare to find circumstances in natural populations where we can actually observe significant mortality events (Shine & Mason, 2004).

Notwithstanding, in Colombia, due to great expansion of oil palm plantations on the last three decades, it have been generate an unusual scenario, in which an exceptionally high concentration of snakes inhabit side-by-side with a blooming human workforce has emerged (Lynch, 2015). This provides an appropriate scenario to evaluate human-snake conflict. Thereby, I have taken advantage of this singular opportunity to test the hypothesis that intentional snake killing by peasants and field workers represents a significant threat for snake conservation (Lynch, 2012).

In the present chapther, I describe the results obteined from a demographic assessment of intentional snake killing over a population of the semifossorial snake *Ninia atrata* that inhabits an oil palm plantation located in the municipality of San Martin (Meta). The predictions that will be tested were based on hypotheses proposed by Lynch (2012) who suggests that intentional snake killing generates a survival decrease on wild snake populations, by adding an extrinsic source of removal of individuals to the existing natural sources of mortality. Hence, if snake populations are threatened due to the intentional snake killing by field workers, we would expect that first, increasing intentional snake killing rates will decrease significantly the population growth rate (λ). Second, an increase in the intentional snake killing rate will produce a damping ratio >1. Finally, the mean life expectancy must be lower in scenarios with low snake killing rate and higher in scnarios with high snake killig rate. The outcomes of the present work were analyzed taking in account their direct implications for snake conservation planning, to better understand the processes involved in snakes population declines due to human activities.

8.3 Methods

8.3.1 Study species

Ninia atrata is a small semifossorial snake (males SVL = 110–323 mm; female SVL = 112–426 mm) widespread in the Neotropical region, ranging from western Panama, Colombia, Ecuador, Venezuela to Trinidad and Tobago, at altitudes between 0 and 1500 ma.s.l (McCranie and Wilson, 1995; Savage, 2002; Angarita-Sierra, 2009, 2014). It exhibits the typical reproductive patterns reported in tropical snakes showing multiple clutches, high mating frequency and continuous sperm production along the year. The reproductive cycles between sexes are different, being cyclical in females, and a continuous cyclical in males with earlier sexual maturation than females (See epigraph 6.1). Moreover, *Ninia atrata* is snail eater snake, with intersexual dietary divergence. Females feed mainly snails, while males have a moderately generalized diet, including slugs, earthworms and leeches (See epigraph 6.2).

The choice of this semifossorial snake as a study system for the question of interest was based on the following criteria: i) Abundance. According to Lynch (2015) *Ninia atrata* was the most abundant species among the 35 species inhabiting oil palm plantations in Colombia, especially at plantations located in the Orinoquia region. ii) High ecosystem representativeness. *Ninia atrata* inhabits leaf litter in almost all Colombian habitats, including the Amazonian and Chocoan rainforests, the evergreen forest of the main Andean rivers, the Orinoquian savannas, and the xerophitic forest at the Caribbean coast (Hallowell, 1845; McCranie & Wilson, 1995; Rangel-Ch, 2004; 2014; Angarita-Sierra, 2009; 2014; Medina-Rangel, 2015; Mesa-Joya, 2015). This species has a high tolerance to disturbed or transformed habitats such as annual crops, pastures, coffee and cacao crops, oil palm plantations and people’s dooryards (Angarita-Sierra, 2015). (iii) High probability of encounter and capture. This snake is relatively easy to find, capture and handle in oil palm plantations. Lynch (2015) reported the highest encounter probabilities for this species at the study area. All of these features make *Ninia atrata* a suitable species to be employed in mark-recapture techniques oriented to estimate survival, growth and fecundity vital rates.

8.3.2 Study area and data collection

Fieldwork was carried out in oil palm plantations of the company PALMASOL S.A. at vereda La Castañeda, municipality of San Martin, department of Meta-Colombia (3°31´46, 6” N; 73°32´15, 3” W). The plantation is located on the piedmont forests of the eastern slopes of the Cordillera Oriental, as well as on high savanna plateaus. Annual rainfall at the site is 3,070 mm (Figure 1Figure 1. Study area. Oil palm plantation (*Elaeis guineensis* Jacq 1897) of PALMASOL S.A. Batches 8, 9, 13 and 15b in Red.). This region is characterized by having monomodal climate with rainy season occurring between April to mid-November, and Dry season begins in the mid-November until March. Climatic variability between years was categorized as good and bad, where good years represent the sampling period from August 2014 to December 2015 without El Niño–Southern Oscillation (ENSO) effects, while bad years represent the sampling period from Jan 2016 to April 2017 under ENSO effects

Sampling was conducted monthly from 7:30 to 17:30 during three sampling days, on period 2014-2017, in one production batch of *Elaeis guineensis* (Jacq 1897) palm between 32 and 36 years old, arranged in parallel lines (Figure 1). However, due to logistical constrains three visits were not made (Supplement 4). Hence, the inter-sampling period ranges between 23 and 60 days. All individuals of *N. atrata* were found by systematically removing piles of palm leaves. Once snakes were caught they were measured (snout–vent length= SVL; Tail length= TL), weighed (Mass), and their health condition, sex and umbilicus scar were registered. At each sampling period, environmental and microhabitats temperature and relative humidity were recorded using thermo-hygrometers (model EBI 20-TH1 Ebro®). Reproductive features of females were used to build fecundity functions following the procedures were described in epigraph 6.1.3.

8.3.3 Mark-recapture experiment and vital rates modeling

Marking procedures follow Dorcas & Willson (2006) where the ventral scales were branded from posterior to anterior, being the anterior scale to the anal plate the first mark point. Furthermore, the anterior portion of the ventral scale was branded and extended the mark diagonally onto adjoining lateral scales using an Aaron Medical Change-A-Tip cautery unit Bovie® (Winne, et al., 2006). Finally, an antibacterial, antifungal and anti-inflammatory ointment was applied on the marked scales (Derma-Vet ointment for veterinary use, Med-Pharmex®). Afterwards, all the individuals branded were released at the same place in which they were captured. All specimens recaptured maintained its mark through whole study, allowing for and accurate identification.

The integral projection models (IPMs) are built on continuous character-demography functions that capture births, deaths, immigration, and emigration processes (Smallegange & Colson, 2013). Hence, the IPM keystone is the vital rates modeling. Each of the above functions represents one or more of the vital rates. These functions are used to build the IPM using the outputs (the coefficients) from regression models that employed the body mass as state variable (Merow, et al., 2014). Body mass was chosen based on the prior results obtained in the reproductive phenology, feeding and survival assessments in which body mass was the common variable that “best” explains each vital rate (see epigraphs 6.1 and 6.2). However, given that SVL also showed to be an explanatory variable of survival, an IPM model was built in order to make comparisons between these morphological explanatory variables (Supplement 8).

- Growth

Mark-recapture data was used to estimate growth rate based on relationship of the body mass and SVL at first capture occasion at t_0, and the change of these traits at the recapture occasion at $t_{+1,}$ considering the time lap between t_0 and $t_{+1.}$ To estimate the growth rate the growth change between t_0 and t_{+1} was calculated employing the equation (Equation 6)

$$\Delta G = \frac{G_{t+1} - G_{t0}}{t_{lap}}$$

Equation 6 Growth shift. Where ΔG denotes growth shift between t_0 and $t_{+1,}$ G_{t0} is SVL in the first capture occasion, G_{t+1} is SVL in first recapture occasion, and t_{lap} is time lap in days between first capture and recapture occasion.

Second, linear regression models were carried out using the software Rwizard version 2.3 (Guisande-Gonzáles, *et al.,* 2014) to describe the type of function that best fits with the relationship between Log ΔG and Log $\bar{G}$ (Body mass mean between the first capture and recapture occasion). For each model R^2 was calculated as a measure of fit. Besides, the assumptions of normality, autocorrelation, and homoscedasticity of each model were assessed using Kolmogorov–Smirnov’s test, Durbin–Watson test and Breusch–Pagan test, respectively. Finally, the function that best fits with the relationship between ΔG and $\bar{G}$ was selected as the growth vital rate (Figure 26A).

- Apparent Survival

The mark-recapture data were used to estimate survival rate by likelihood methods, logistic regression and Cormack-Jolly-Seber (CJS) model implemented in MARK (White & Burnham, 1999). A total of 44 models were performed (Supplement 5-7). The fit of each model was assessed using the adjusted Akaike information criterion for small sample sizes (AICc) (Akaike, 1973; Caswell & Fujiwara, 2004). The AICc is a measure of model likelihood and parsimony, and the smallest value indicates the best fitting model. A difference in AICc values (∆AICc) larger than 2 indicates a real difference of fit to the data between models (White & Burnham, 1999; Pérez-Mendoza & Zúñiga-Vega, 2014). I report ∆AICc for each competing model with respect to the best-fitting model (Figure 26B). Several abiotic and biotic variables such as: temperature and relative humidity of the environment (TH), temperature and relative humidity microhabitat (TH1), and seasonality total food, snail abundance, earthworm abundance were employed as covariates in order to explore the factors that influence survival.

- Fecundity

Fecundity vital rate estimation was based on regression models that describe the type of function that “best” fits with relationship between female body mass and clutch size (Figure 26C). Given that the lightest female with vitellogenic follicles, indicating sexual maturity, was 8.3 gr, the regression models only considered females that crossed this threshold (see epigraph 6.1). Clutch size was considered as the number of oviductal eggs, or the number the eggs laid by each female. Regression models were carried out using the software Rwizard version 2.3 (Guisande-Gonzáles, *et al.,* 2014) through the following steps. First, the square root or natural logarithm of clutch size observed and body mass was found or transformed using Tukey's staircase transformation method described by Erickson and Nosanchuk (1977). Second, assumptions of normality, autocorrelation, and homoscedasticity were evaluated using Kolmogorov–Smirnov’s test, Durbin–Watson test and Breusch–Pagan test, respectively. Third, the function that “best” fits with the relationship between female body mass and clutch size was selected as the fecundity vital rate. Also, fecundity vital rate considered the size distribution of recruits observed at time *t*+1. Therefore, recruits mass distribution observed were compared with theoretical distributions (uniform, normal, exponential, bootstrap, logistic, beta, Log-normal, gamma, and weibull) through a skewness-kurtosis graph (Cullen & Frey, 1999). Finally, to select the “best” fitted recruit distribution, a Kolmogorov–Smirnov test was performed as a measure of goodness-of-fit (Figure 26 C-D).

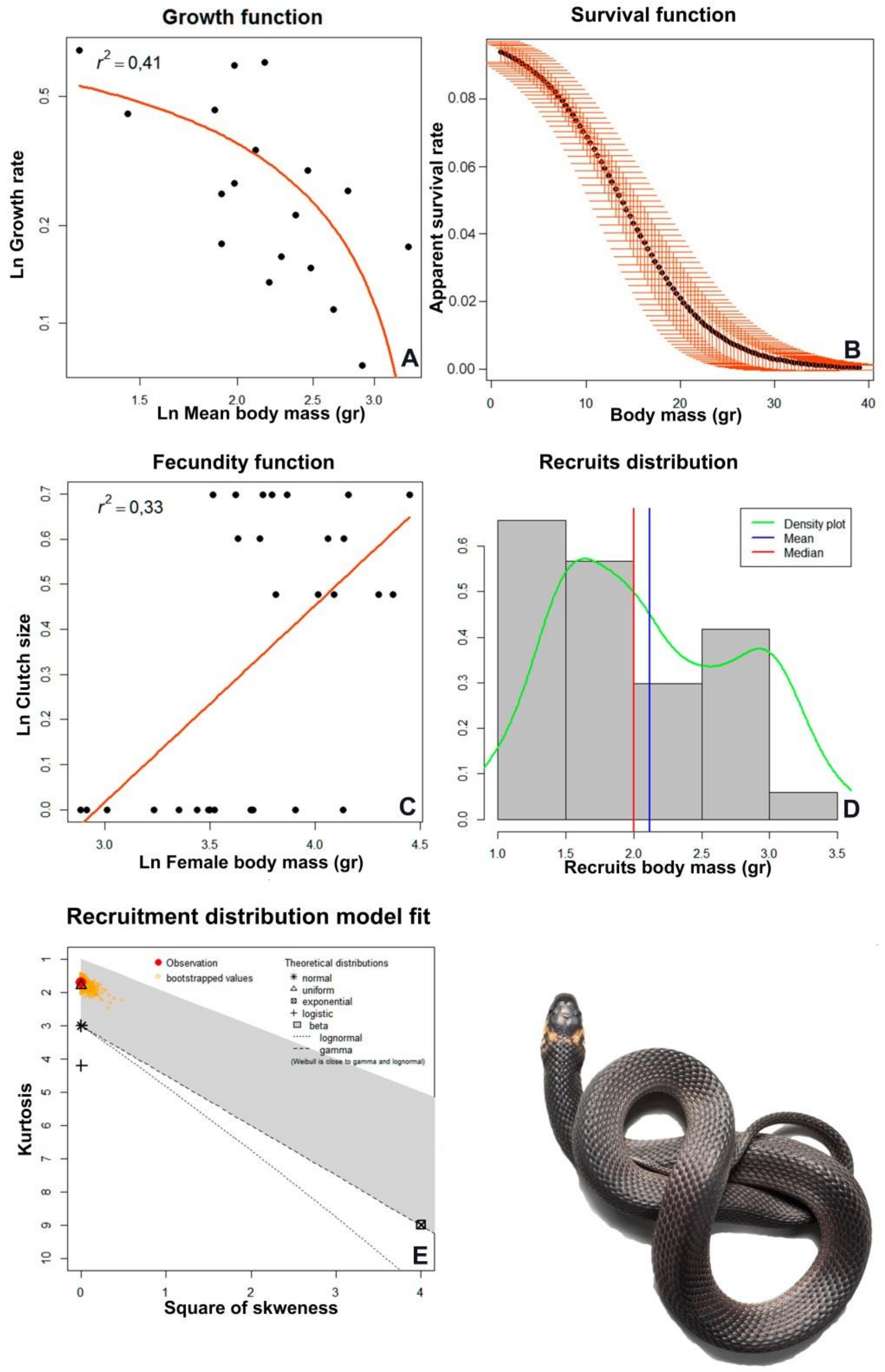

Figure 26. Fitting of growth, survival, fecundity functions, and recruits size distribution of *Ninia atrata*. A) The data on year-to-year changes in body length relative to body mass mean between the first capture and recapture occasion. B) Apparent Survival function estimated through a logistic regression under the model Cormack-Jolly-Seber. C) Linear regression model that describes the relation between female body mass and clutch size. D) Recruits body mass distribution. E) Fitting of recruit's body mass distribution with theoretical distributions.

8.3.4 Integral projection model (IPM)

The integral projection model describes how a population structured by a continuous individual-level state variable changes in discrete time. (Easterling, *et al.,* 2000). The core of an IPM is the kernel: a function that describes how the state of an individual at one time dictates its state and that of its offspring at some future time (Merow, *et al.,* 2014). The kernel is composed by functions that describe the vital rates such as fecundity *f(x, y),* survival and growth *p*(*x, y*) (Equation 7)

$$K(x,y) = p(x,y) + f(x,y)$$

Equation 7. Kernel formula. Where *K*(x, y), denote kernel function that describe all possible transitions from size *x* to size *y*.

The function *p*(*x, y*) incorporates both growth and survival. Particularly, the survival-growth function can be expressed as *p*(*x, y*) = *s*(*y*) *g*(x | y), being *s*(*y*) the survival function that describes the probability that an individual will survive to t_{+1} which dependent of the individual mass at t_0; *g*(*x* | *y*) represents the growth function that describes the probability density of mass *y* that an individual of mass *x* can grow during one time step.

Likewise, the fecundity function *f*(*x, y*) can be expressed as *f*(*x, y*) = *f*(x) f(y), where *f*(x) describes the probability of egg production as a function of female of mass x, and f(y) describes the mass distribution of recruits observed at time $t_{+1.}$ Therefore, the IPM kernel is composed by intercepts and slopes of the vital rate functions obtained through the regression models. Once built the kernel final step is to describe how a *Ninia atrata* population structured by body mass changes in a year. For that, the integral projection model for the number of individuals of size *y* at time t_{+1} is then

$$n(y, t_{+1}) = \int_{\Omega} K(x,y) n_t\ (x,t) dx$$

Equation 8. Integral projection model (Easterling, 1998)

Where $n(y, t_{+1})$ denote the continuous function of y that describes the population size distribution at time $t_{+1;}$ $n_t(x, t)$ represents the number of size x individuals at time t; and Ω represent all the possible sizes to be integrated. Due to the integration is solved throughout a numerical method; the midpoint rule was used to estimate the area under a curve (Merow, et al., 2014). All development of the IPM analyses was done using the software Rwizard 2.3 (Guisande-Gonzáles, *et al.,* 2014) and the r packge IPMpack (Metcalf, et al., 2014).

The simplest information related to asymptotic dynamics provided by traditional matrix projections models (MPMs) such as the population growth rate (λ), stable population structure and reproductive value can also be obtained by IPM in a similar way. The IPM has a dominant eigenvalue λ that represents the population's asymptotic growth rate, under biological assumptions that are no more restrictive than those required in the MPMs (Caswell, 2001). Corresponding to λ are dominant right and left eigenvectors w(x) and v(x), and, as MPMs, which give the stable mass distribution and mass-specific reproductive value, respectively (Easterling, et al., 2000). The development and methods for computing the dominant eigenvalue and corresponding eigenvectors are described in supplement 10.

8.3.5 Perturbation analyses

The sensitivity and elasticity formulas for IPM are very similar to those of a matrix model (Caswell, 2001). Thus, I follwed the procedures described by Easterling, et al (2000) to analyse sensitivity and elasticity of the growth rate to small changes in survivorships and fecundities. Because the fecundities and survivorships in the integral projection model are represented by a surface rather than a matrix, sensitivity analysis for the model involves determining the sensitivity of the dominant eigenvalue to changes in the survivorship/fecundity surface k(y, x) over a small region centered over each point (y, x), as follow:

$$s(z_1\,,\,z_2) = \frac{\partial\lambda}{\partial k(z_1\,,z_2)} = \frac{v(z_1)w(z_2)}{\langle\,\mathrm{w},\mathrm{v}\rangle}$$

Equation 9. Sensitivity analysis (Easterling, et al., 2000)

Where s (z_1, z_2) is the sensitivity of λ to small changes in the *k* (*y, x*) values near (z_1, z_2). The corresponding elasticity estimates are therefore given by

$$e(z_1\,,\,z_2) = \frac{k(z_1\,,\,z_2)}{\lambda} \times \frac{v(z_1)w(z_2)}{\langle\,\mathrm{w},\mathrm{v}\rangle}$$

Equation 10. Elasticity analysis (Kroon, et al., 1986, Easterling, et al., 2000)

The elasticity function integrates to unity, which correspond to the sum to unity in the matrix projection model (Easterling, 1998). However, the IPM interpretation of the sensitivity (Equation. 9) is slightly different than in the matrix model. It should be interpreted as the relative sensitivity of λ to changes in different mass-specific transition rates (Easterling, et al 2000).

In addition to sensitivity analyses, and in order to assess the influence of intentional snake killing on the *Ninia atrata* population under study, a perturbation analysis including the snake killing rate observed on the oil palm plantation was performed. Hence, I examined the consequences of four killing scenarios that have direct effect on survival rate. First, no snake-killing scenario, which is the results of adding the observed relative number of snakes killed. Second, intensive snake-killing scenario, which result from increasing up 50% the killing rate observed. Third, population size increases scenario, which results of adding up 50% of the relative number of observed snakes killed observed. Additionally, the snake killing rate estimated by Lynch et al (2014) was considered as fourth scenario (Supplement 9).

This additional perturbation analysis was accomplished modifying the intercept of the survival function according to the snake killing rate of each scenario. The snake mortality records as result from human activities were obtained from 167 surveys carried out during 2016-2017 (see epigraph 7). Given that the patterns of intentional snake killing at oil palm plantation do not have selective behavior (see epigraph 7), the intercept of the survival function was modified considering that this source of mortality has the same rate across all the segments of the population (neonates, adults, females, males, etc.). Finally, damping ratio was employed as measurement of the population resilience to the intentional snake killing effects on the different scenarios assessed (Stott, et al., 2011)

8.4 Results

8.4.1 Demographic features of *Ninia atrata*

During the sampling period 349 specimens of *Ninia atrata* were marked (males=160; females=189). Twenty six snakes were recaptured (13 males and 13 females; 7.45%) of which one male and two females were recaptured twice. A significant decrease of number of individuals was observed during bad climatic years (χ^2= 180.72, P< 0.001, n= 349). Likewise, the differences in recaptured snakes between seasons were significant being higher on rainy season than dry season (χ^2= 5.54, P< 0.018, n= 26). In contrast, the number of recaptured snakes (χ^2= 1.38, P= 0.24, n= 26) as well as the snake killing rate estimated (3.7–4.3 snakes killed/monthly) did not show significant differences between climatic years (χ^2= 0.18, P= 0.73, n= 33).

The population structure is mainly composed by light weighted snakes which cause a marked positive skewness (Figure 27A). Also, the population structure showed a conspicuous difference between sexes, in which females have a positive skewness and mesokurtic distribution dominated by light weighted snakes with a mode of 3 gr (neonates), while males exhibited a negative skewness and platykurtic distribution dominated by moderate weighted snakes with a mode of 11 gr (adults) (Figure 27 B-C). Similarly, noticeable differences on the population structure shape between climatic years were observed, having a positive skewness and mesokurtic distribution on good years (Figure 27 F-G), while a symmetric and leptokurtic distribution on bad years, dominated by adult individuals of moderate body mass with a mode of 10g (Supplement 8**¡Error! No se encuentra el origen de la referencia.**). However, these differences between sexes and climatic years were not significant (W_{sexes}= 16650, P=0.10; $W_{Climatic\ years}$= 7982, P=0.20).

In contrast, significant differences in the population structure between seasons were found (W=16712, P< 0.0001), the population structure is dominated by light weighted snakes with a mode of 1.5 gr (neonates) during the dry season, whereas the population structure was composed mainly by moderate and heavy weighted snakes (adults) on rainy seasons (Figure 27 D-E). This result was expected due to the fact that the greatest recruitment peak occurs on mid-dry season (see epigraph 6.1). Moreover, neonate body mass distribution followed a closely uniform distribution with a low skewness and kurtiosis with a body mass mean of 2.33 ±0.75 gr (Figure 26D-E), however, not showing good goodness-of-fit (H=0.19, P<0.05) to any “common” univariate parametric distributions.

On the other hand, the growth function provided a good fit to the observed shift in body mass (Table 10). This model showed a fast growth tendency on light weighted snakes (neonates and juveniles), decreasing gradually with the increment of the snakes’ body mass ($\bar{x}_{daily\ growth\ shift}$ = 0.024 g) without significant differences between sexes (t= -0.065, P= 0.95, n= 26) (Figure 26AFigure 26). Analyses of covariance of daily growth rate with sex as factor, and SVL as covariate, gave similar results in where the relationship between daily growth rate and mean body mass did not differ in slopes between sexes ($F_{SVL[2,20]}$= 0.23, P= 0.80; $F_{Body\ mass[2,20]=}$ 0.52, P= 0.60), but did differ in the intercepts ($F_{SVL[2,20]}$= 0.23, P< 0.01; $F_{Body\ mass[2,20]=}$ 0.52, P< 0.0001).

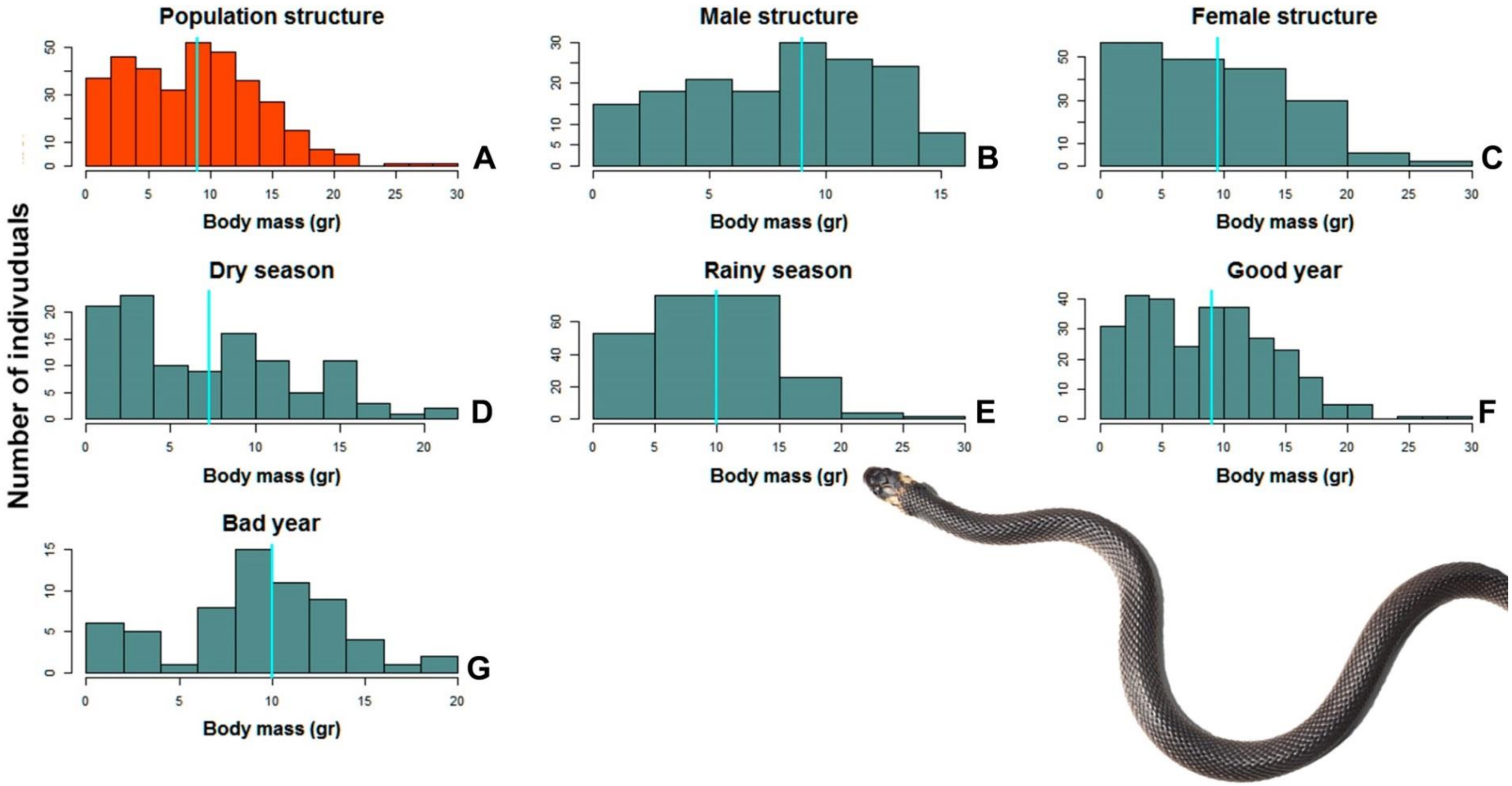

Figure 27. Population structure of *Ninia atrata*. A) Population structure of *Ninia atrata* observed during 2014-2017. B-C) Population structure by sexes. D-E) Population structure by seasons. F-G) Population structure by climatic years. Cyan line represents median value of each distribution

Likewise, the fecundity function showed a good fit between female body mass and clutch size (Table 10). This model indicates a positive relationship between body mass and clutch size, in which clutch size increase with the gain of body mass (Figure 26C). Nonetheless, given that female reproductive output is mediated by other factors such as secondary follicle number, stomach bolus volume, or fat body area (see epigraph 6.1), the goodness of fit of 33% is a partial value of the clutch size variability observed. On the other hand, the sex ratio variation observed (0.16) did not have significant differences between season (χ^2= 2.13, *P*= 0.14, n= 349) or climatic years (χ^2 = 0.93, *P*= 0.33, n= 349) indicating that males and females have the same capture chance. In contrast, on years with ENSO effects the number of neonates detected decline fourteen times passing from 57 records during good years to four records during bad years (χ^2 = 10.557, *P*= 0.001). However, it was not possible to detect a predictive relationship between capture probability and sexes based on mark-recapture, given that all models that included sex had no support (Supplement 6). Further, females with sperm inside the infundibulum or oviduct, gravid females and clutches were almost observed throughout all the year (except on December), indicating that mating, multiple clutches and recruitment are continuous throughout year, with an average clutch size per female of 2.44 ±1.02 eggs (ranging1 to 4 eggs).

Table 10. Statistical models and parameter estimates describing the demographic process of *Ninia atrata*. The models are function of body mass x values in parentheses are standard errors of parameter estimates. The predicted values are the conditional mean $\bar{y}$, the survival probability s, and fecundity $\overline{fn}$. Nor.test= Kolmogorov–Smirnov's test for normality, Hom.test= Breusch–Pagan test for homoscedasticity, and Aut.test= Durbin–Watson test for autocorrelation.

Vital rate functions	Model
Growth (mass)	$\bar{y} = 0.84(.16) - 0.24(0.073)x$, $R^2 = 0.41$, $P = 0.004$, $N = 24$. $Nor.test = 0.09$, $Hom.test = 0.48$, $Aut.test = 0.50$
Survival (mass)	Logit(s)= 0,995(0.45) -0,25(0.51)x, 95% CI intercept= 0.40—0.98, 95% CI slope= 0.13—0.43
Recruit distribution (mass)	Uniform with mean =2.33 , *standard deviation*= 0.75, *max*= 3.5, *min*=1, *Skewness*= 0.03, *Kurtosis*= 1.71
Fecundity (mass)	$\overline{fn} = -1.30(.45) + 0.44(0.012)x$, $R^2 = 0.33$, $P = 0.001$, $N = 32$. $Nor.test = 0.82$, $Hom.test = 0.07$, $Aut.test = 0.70$

A total of 44 survival models were explored of which the most parsimonious survival models derived from the Cormack–Jolly–Seber method were those that considered SVL and the body mass as covariable (AICc $_{\text{SVL}}$ weight= 0.574; AICc $_{\text{body mass}}$ weight= 0.382). The survival model that consider the body mass estimated an annual survival of 0.084 (0.014-0.37, 95%CI, n= 26) while the survival model that considers SVL estimated an annual survival of 0.093 (0.012-0.34, 95%CI, n= 26). However, both showed a strong negative relationship suggesting that with increasing snake body mass or SVL, the chances of survival decrease (Figure 26B). I failed to detect a predictive relationship for survival and time, given that all models that included time or changes with time had no support. Likewise, the models that considered abiotic or biotic determinates as co-variables were not supported (Supplement 6-7).

8.4.2 Demographic analysis of the model

The IPM kernel depicts that highest transition probabilities were observed at fecundity vital rate. Besides, the asymptotic analyses showed that the estimated population growth rate from the fitted integral model is λ=0.895, having a stable mass distribution heavily skewed towards light weighted snakes, which is similar in shape to the initial mass distribution observed. However, the projected stable mass distribution was significantly different from the observed structure population (χ^2= 9.37, P< 0.001, n= 2) indicating that population structure changes drastically from year to year. The reproductive value indicates that heavy weighted snakes (mainly reproductive females) are the individuals with the strongest contribution to long-term population size (Figure 28).

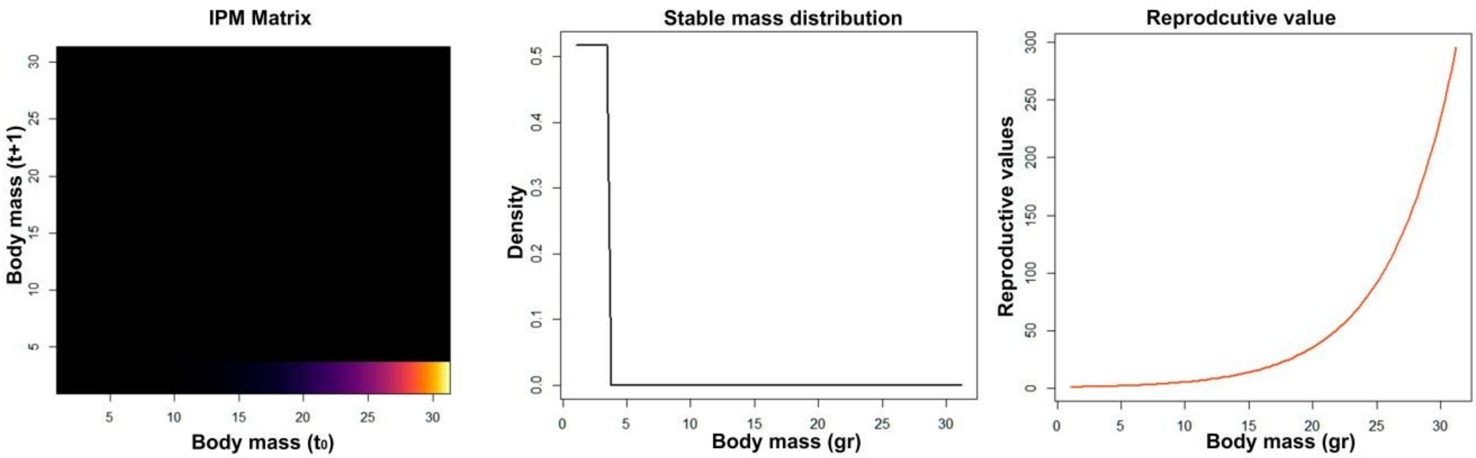

Figure 28. A 100-stage integral projection model of *Ninia atrata* population under study. A) Heat map of the high resolution kernel that describes the transitions of a snake of mass "x" at time t_0 during a projection interval to time t_{+1}. B) Right eigenvector (w_1) of the IPM matrix. C) Left eigenvector (v_1) of the IPM matrix.

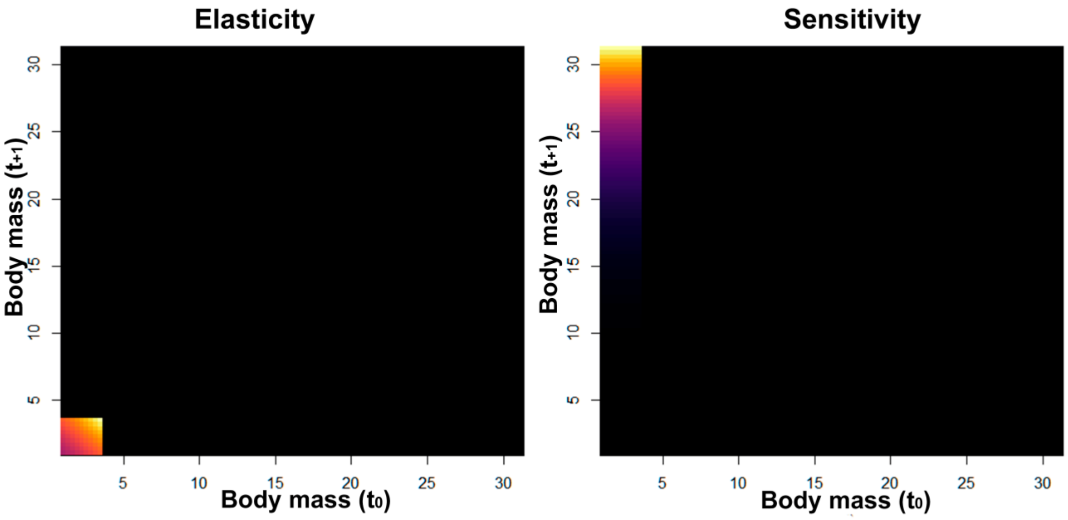

Figure 29. Heat maps of elasticities and sensitivities. Larger values were represented by lighter pixels (white, yellow, and light orange) and smaller values by darker pixels (orange, purple and black) through a color scale inferno of the R package "viridis" (Garnier, et al., 2017).

The sensitivity and elasticity analyses indicates that *Ninia atrata* population growth rate is far more sensitive to changes in recruitment and reproduction rates than to either growth or survival rates (Figure 29). Given that sensitivity surface is determined by the stable mass structure and reproductive values (Equation 9), the sensitivity's heat map surface shows a sharp peak represented by lighter pixels at heavy weighted snakes (mainly adult females). Thus, the integral model predicts a lower relative reproductive value for light weighted snakes, and therefore assigns lower sensitivity to transitions into the lighter mass classes. Likewise, the lager elasticities were assigned to light weighted snakes (neonates) due that elasticity surface is proportional to the product of the sensitivity surface and the kernel. Hence, the population growth rate of *Ninia atrata* was dependent on the light weighted snakes (neonates).

Consistently with the sensitivity analyses, the snake killing rates assessed throughout the four perturbation scenarios did not show significant changes on population growth rate because the survival vital rate has a minor contribution to λ (Figure 30A). Also, simulated populations with the same total initial size but modified the intercept of survival function according to each killing scenario, showed identical trajectories reporting a λ=0.895, and as a result, a damping ratio equal to 1 (Supplement 9). Likewise, the simulated populations depicted the same mean life expectancy tendency without leaning toward any of the predicted scenarios (Figure 30B).

8.5 Discussion

Despite the alarming annual snake killing rates estimated by Lynch (2012) and Lynch et al (2014), as well as the snake killing rates simulated under the scenarios assessed, the *Ninia atrata* population under study seems to escape from a certain death according with the results obtained from IPMs. The idea that intentional snake killing has a deep impact on snake population viability, comes from the common sense impression that removal of individuals from population causes a proportional numeric response on the population size (Figure 30A).

However, the results pointed out that this impression does not apply in the broad sense.

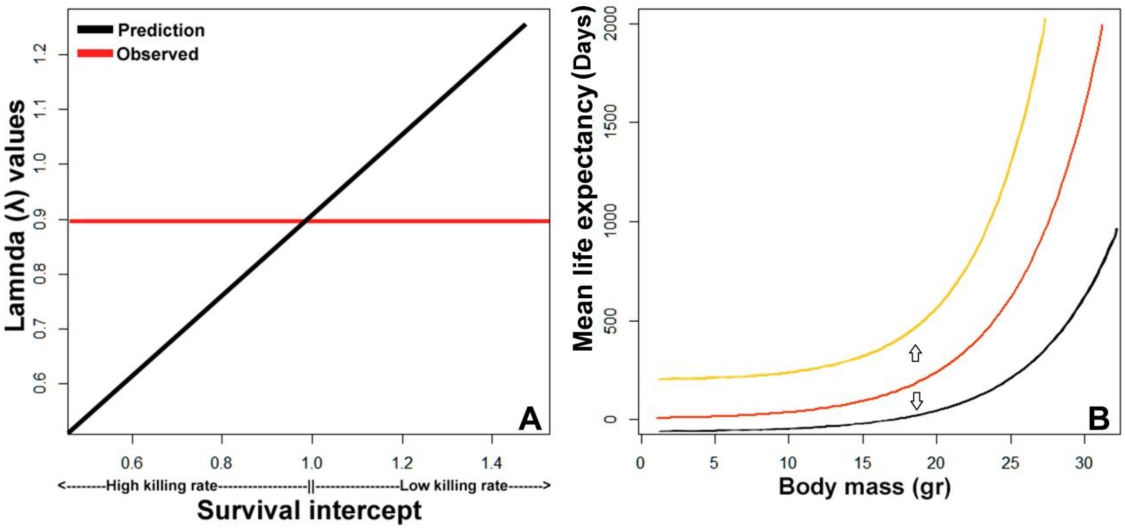

Figure 30. Comparison between results observed and predictions. A) Red line: λ values observed according the four perturbation scenarios assessed. Black line: expected values of λ according to the prediction. B) Red line: Life mean expectancy observed according the four perturbation scenarios assessed. Black line: Mean life expectancy expected under scenarios with high killing rate. Yellow line: Life mean expectancy expected under scenarios with low killing rate. Arrows point out the expected tendencies.

Particular demographic features of the *N. atrata* population such as: (I) highest reproductive values allocated to heavy weighted snakes (mainly reproductive females), (II) a population structure dominated by light weighted snakes (neonates), (III) a high and continuous reproductive activity throughout year, (IV) a survival pattern that resembles Type I survival curve described by Pearl (1928), (V) significant differences between population structure observed and projected, and, (VI) a population growth rate away from equilibrium, suggests that *N. atrata* is a short-lived snake with population dynamics leaning towards the fast end of the “slow–fast'' continuum of the life history pattern (Franco & Silvertown, 2004, Dobson, 2007).

Consistently, the *Ninia atrata* population under study exemplifies the typical life history pattern observed in short-lived species with a high adult mortality rate compensated by high rates of recruitment, mainly by smaller individuals, as well as a high reproductive effort allocated at each of its few reproductive occasions. All these lead to a low variance in reproduction while survival is highly variable (Gaillard & Yoccoz, 2003, Franco & Silvertown, 2004, Hemel, et al., 2010). Thus, the intentional killing as an additional source of mortality to the existing natural sources does not have significant effects on its population dynamics or on the demographic outputs. This result supports the hypothesis that species with fast life histories are less vulnerable to extinction under scenarios of human disturbance (Weeb, et al., 2002).

Additionally, the lack of effects on λ, as well as mean life expectancy by intentional snake killing, can also be explained by the patterns of the human-snake conflict. This source of snake mortality takes distance from similar sources, such as harvesting. Firstly, fieldworkers do not a selective behavior when they decide to kill a snake, most cases, reducing the behavior to snake seen snake killed [versus direct selection of species, size classes or sex at harvesting scenarios (Van Cao, et al., 2014)]. Secondly, encounters of people and snakes occur during daily farm activities as unexpected or unplanned event [versus planning hunt activities seeking an optimal harvest strategy (Brooks, et al., 2010)]. Finally, since the intentional snake killing is an uncertain event and is influenced by the field task, gender, education level, and the way in which field workers experienced fear (see epigraph 7), it is unlikely that this source of mortality has a focal effect on any population segment or demographic processes provoking a direct demographic response. In contrast, at harvesting scenarios, the addressed selection of one segment of the population due the commercial harvest requirements, provokes a direct demographic response such as changes on size at maturity, changes on population structure, body size, fecundity rate, among others (Brooks, et al., 2010, Coock, et al., 2014).

These findings have important general implications for the planning and management strategies for snake conservation. Firstly, to promote life history traits studies is an essential need towards a suitable categorization of the snake species threatened by anthropogenic activities. Since the viability of any biological population depends of the balance between rates of production of new individuals (reproduction) and the rates of loss (mortality) (Shine & Bonnet, 2000), understanding of the snake life history strategies help us to identify which snake populations have highest risk of extinction against different anthropogenic sources of mortality. For example, Weeb, et al (2002) found that the endangered snake *Hoplocephalus bungaroides* (Schlegel, 1837) was considerably more sensitive to habitat loss due to urbanization than the sympatric snake *Cryptophis nigrescens* (Güther, 1862), despite that both elapid species are closely phylogenetic ally and share similar biological traits (both are nocturnal, viviparous and with similar in body size) because their life history strategies were different, being *H. bungaroides* a long-lived species, while *C. nigrescens* a short-lived species.

Similarly, the short-lived strategy observed in the *N. atrata* population allows it to be insensitive to the addition of an extrinsic source of removal of individuals by intentional killing, but at same time, makes it sensitive to other anthropogenic sources of mortality such as habitat loss. Neonates of *N. atrata* showed a highly sensitve to changes in prey availiblity and abundance, as well as changes on temperature and relative humidity of the environment, and microhabitat quality (see epigraph 6). Therefore, according with elasticity analysis, the IPM model predicts that during the establishment and renovation of an oil palm plantation, or any extensive monoculture, *N. atrata* populations should show a conspicuous decrease of λ due to the great disturbance caused by clearing of the land by removal of vegetation and destruction of ground litter (mechanically or with fire), which in turn, altered the determinant factors of the recruitment of new individuals.

Thus, information about snake life history traits helps us to build a reliable ecological knowledge that allows to differentiate between threatened an nonthreatened taxa through any trait correlated with a source of anthropogenic mortality (Shine & Bonnet, 2000). Besides, this approach provides a robust tool that complements the traditional criteria employed to classify some taxon in IUCN threat categories, since in practice, the decision is often reduced to assessing only the degree of endemism and distribution by a criteria given by local experts due to lack of life history detailed information (Morales-Betancourt, et al., 2015).

Secondly, the present results highlight that snake populations can persist successfully in highly modified environments such as oil palm plantations. Although monocultures depend on fundamental ecosystem services such as water and soil (Butler, et al., 2009), they also provide refuge and food to local wildlife, as long as they implement good agricultural practices. Therefore, planners and stakeholders advocating for snake conservation must consider the extensive monocultures in the designs of their strategies and lines of action. Minor changes to agricultural practices such as the maintenance of shrubby borders around plantations that allow the conectivity between the monocultures and forest have proven to be a critical factor to maintain the reproductive processes of snake population that inhabit rural lanscapes (Shine & Fitzgerald, 1996, Shine & Bonnet, 2000). Particularly, oil plam monocultures have internal practices such as the stacking of palm leaves derived from the pruning cycle that acting as artificial shelters, protect at least 25% of the local snake communities (Lynch, 2015) Therefore, given that oil palm agriculture is rapidly expanding in the Neotropics in natural and seminatural habitats (Pardo, et al., 2015), planners and stakeholders must link with this industry in order to implement management actions that minimize the extinction probabilities of the snake populations, as well as protecting the wildlife that inhabit the monocultures. The implementation of these actions must to be seen as payments for ecosystem services used in the development of its agroindustrial activities, as well as a compensation for the destruction of natural habitats during the establishment and renovation of its monocultures.

Finally, the extreme changes on weather due to ENSO effects caused outstanding effects on *N. atrata* population in demographic traits such as recruitment and population structure (Figure 27). Indeed, an evident population´s numerical response was observed between good and bad climatic years (Figure

2), suggesting that the λ value estimated by IPM showing a population decline was related with the beginning of the study when the population was at its peak (good climatic years). Therefore, the IPM model captured the effect of environmental extremes between climatic years in which recruitment dropped dramatically during bad years, which likely caused a λ value < 1 and the decreasing on population size observed. Regrettably, this climatic effect could not be directly tested through this IPM because of the lack of robust mark-recapture data between climatic years.

Notwithstanding, this result warns us that the effect of climate variation on population dynamics depend on population composition given that it affects each segments of the population in different ways. Similar results have been seen on mammals and birds (Coulson, et al., 2001, Alrwegg, et al., 2003), as well as reptiles from temperate and tropical regions (Laurie & Brown, 1990, Altwegg, et al., 2005, Ujvari, et al., 2015) suggesting that interaction between climate and life history is one the most important drivers of the population structure, and reproduction success. This is particulary important to snakes populations, due to its deep dependece of temperature in almost all of its biological proceses (Shine & Bonnet, 2000). Therefore, conservation strategies that seek to incorporate management actions to reduce the impacts of the climate changes on snake populations, must consider how seasonal shifts or weather extremes increase the snake mortality risk towards natural (e.g. predation and famine) or anthropogenic sources of mortality, taking into account each segment of the population.

It is difficult to generalize the results of this study to natural ecosystems or *N. atrata* populations inhabiting at natural environments. Even so, this study allows us to gain understanding of the processes involved on intentional snake killing, and reduces knowledge gaps around the sources of snake mortality that could causes their population decline.

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9. Chapter 4: Conclusions and recommendations

Some of the incipient snake conservation programs in the tropical regions have considered the intentional snake killing as a threat, even though in most cases no robust evidence relates this source of mortality with the snake population decline (França & Araújo, 2006, Lynch, et al., 2014). However, the lack of basic information on the life history traits of most snake species, as well as the lack of support and interest (financial and political) by decision makers, researchers and the general public, constitute the major impediments to study the sources of snake mortality in a conservation context, and implement the lines of action of the programs for snake conservation (Dood, 1987, Seigel & Mullin, 2009).

The advent of new techniques in biology (e.g. Genomics, molecular biology, proteomics, landscape ecology, among others) over the last four decades have generated an avalanche of knowledge, and a widespread perception among academics and researchers is that natural history studies are dying (Arnold, 2003). This perception seems to have its origin in its descriptive nature, the demanding field work, the slow production of manuscripts and the high costs (Noss, 1996).

Certainly, the descriptive nature of natural history studies has generated a false perception that the investment of financial resources in this discipline is irrelevant, that its results have little impact to applied biology, or that they are obsolete towards the advancement of biological knowledge (Bury, 2006). However, the result of this thesis agrees with by Bartholomew (1986), Green & Losos (1988), Bury, 2006; Arnold (2003) Green (2005), Vitt (2013), among others, who state that natural history studies have been the key to the development of conservation and wildlife management, understanding of the evolution of life as we know it, as well as creating social values which helped us build our societies.

Studies of natural history were the keystone that allowed this thesis to assess one of the poorly explored sources of snake mortality, the intentional snake killing, attaining to unveil the processes involved, and to produce applied biological knowledge for snake conservation.

The primary conclusion from my analysis is that intentional snake killing by field workers does not represent significant threat to viability of the snake populations with fast life histories. Besides, sensitivity of the snake populations towards anthropogenic and natural source of mortality depends deeply of its population structure. Thus, to characterize the basic traits of snake populations such as structure, sex ratio, reproduction and determinants of reproductive output could help us to differentiate between threatened an nonthreatened taxa, with regarding the source of mortality in question.

Some of these basic traits could exhibit biases on the sampling technique employed as well as microhabitat explored. Therefore, before any study, extensive test-sampling must be carried out in order to know the proclivity to find sex-biases or size-biases between samples. In the present study, the sample of snakes collected under piles of palm leaves or epiphytic mattress provides an unbiased sample of overall *Ninia atrata* population structure. This could be achieved thanks to the experience gained through several years working at oil palm plantations, where a lot of microhabitats and techniques were explored, and the oil palm agroecosystem was understood (Lynch, et al., 2014, Lynch, 2015).

Given that El Niño ENSO phenomenom recorded on 2016 was the strongest of the last 20 years, it provokes a deep impact on high savanna plateaus of the Llanos Orientales of Colombia, as well as in the mark-recapture experiment due to the dramatic decrease of number of snakes captured. Therefore, during bad climatic years the probability of recapture decreases considerably, as a consequence of the low number of marked snakes in each sampling occasion. This caused biases on the estimation of the population size given that its determination depends on recapturing individuals within a restricted period soon after marking (Caughley, 1977).

On the other hand, due to logistics and financial constraints, the sampling design considered short sampling occasions (three sampling days) in a relative small period (from Aug 2014 to June 2017). Despite that the IPM method provides a robust estimation from small data sets with short periods of sampling (Metcalf, et al., 2014), the estimation of survival and growth functions depends on recapturing individuals after an extended period since marking (Parker & Plummer, 1987). Hence, the low number of recaptures during short time-laps during the sampling period caused large standard errors on the parameters estimated for these vital rates (Figure 31). Nonetheless, the IPMs and regression models built were capable of capturing the variability observed on the survival and growth vital rates, determining the roll of these demographic processes facing the effects of the intentional snake killing.

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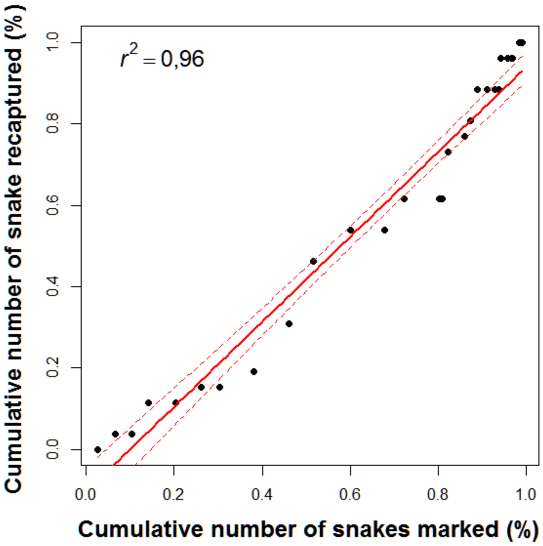

Figure 31. Marked vs. recapture *Ninia atrata* snakes during the sampling period 2014-2017. Red Dashed line represents 95% confidence intervals. Solid red line denotes the linear regression model that describes the relationship between marked and recaptures snakes.

Given the experience acquired during the implementation of mark-recapture experiment to assess the effect of the intentional snake killing, I suggest that robust design models (Pollock, et al., 1990) rather than Cormack-Jolly-Seber models should be employed for future studies. This approach allows the estimation of both survivorship and population size without violating assumptions of either open or closed populations (Dorcas & Willson, 2006). Also, it permits to test temporary emigration, as well as incorporates time-varying capture probability, and heterogeneity. These aspects were detected in this study, but they were unable to evaluate.

Finally, my results indicate that the degree of risk experienced by snakes toward the intentional snake killing varies according to the task developed by field worker. However, it is strongly influence by factors such as the way in which field workers experience fear, gender and education level. These findings have strong impact in the way conservations strategies should be built in order to mitigate the threats for snake conservation, or wildlife in general.

Particularly, oil palm plantations congregate a large number of workers unaware of the snake diversity with which they live daily. Therefore, most of the malicious attitudes towards snakes come from fear of the unknown, of ignorance about the kinds of snakes that could be a real health hazard, and from the traditional division of labors and social organization by genders.

In order to generate actions that contribute to a sustainable and wildlife-friendly agriculture, the palm grower guild, plantation owners and governmental entities must join to seek the management actions that induce a positive attitude of the plantation workforce toward snakes. However, this actions should not be punitive measures (Aldana, 2011), but must focus on teaching environmental values and training in friendly agricultural practices that help to incorporate the idea that snakes are a natural heritage that should be conserved in the collective imaginary of the workforce.

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10. Supplementary information

Supplement 1. Structured survey applied to peasant and fieldworkers of Palmasol S.A.

<table>
<tr><td>NOMBRE</td><td colspan="3"></td><td>ORIGEN</td><td colspan="2"></td><td rowspan="2">EDAD</td><td colspan="2">(1)18-19</td><td>(2)20-24</td><td>(3)25-29</td><td>(4)30-34</td><td>(5)35-39</td><td rowspan="2">Sexo:
(0)Mujer
(1)Hombre</td></tr>
<tr><td>OCUPACIÓN</td><td colspan="3"></td><td>FECHA</td><td colspan="2"></td><td>(6)41-44</td><td>(7)45-49</td><td>(8)50-54</td><td>(9)55-59</td><td>(10)60-64</td><td>(11)>65</td></tr>
<tr><td colspan="4">Pertenece a alguna organización o agremiación</td><td>SI</td><td>NO</td><td colspan="5">Cuál?</td><td colspan="2">Labor que desempeña</td><td colspan="2"></td></tr>
<tr><td>Nivel educativo</td><td>(1)Primaria</td><td>(2)Primaria incompleta</td><td>(3)Bachillerato</td><td>(4)Bachillerato incompleto</td><td>(5)Universitario</td><td>(6)Universitario incompleto</td><td colspan="2">¿Hace cuánto trabaja aquí? (meses)</td><td colspan="2"></td><td colspan="2">Labor/hora/día(tiempo)</td><td colspan="2"></td></tr>
<tr><td colspan="2">Serpientes vistas/ en la última semana</td><td colspan="2"></td><td colspan="2">Serpientes matadas/en la última semana</td><td></td><td>¿Por qué razón mata las serpientes?</td><td>(1)Miedo</td><td>(2)Magico /religioso</td><td>(3)Precausión</td><td>(4)Defensa propia</td><td>(5)Defender a un tercero</td><td>(6)Sin razón</td><td>(7)No las mata</td></tr>
<tr><td colspan="4">¿Dónde vio la serpiente?</td><td>¿Qué estaba haciendo la serpiente cuando la vió?</td><td colspan="4"></td><td></td><td colspan="2" rowspan="2">¿Que hizo la serpiente cuando lo vio a usted?</td><td>(1)Avazo hacia usted</td><td>(2)Atacó</td><td>(3) Lo ignoró</td></tr>
<tr><td rowspan="2">¿Cuál fue su respuesta cuando vio la Serpiente?</td><td>1)Avazo hacia la serpiente</td><td>2)La Atacó</td><td>3)La ignoró</td><td colspan="5">De las siguientes imágenes señale la(s) serpientes que cree son venenosas</td><td></td><td>(4)Huyó</td><td>(5)Se quedó quieta</td><td>(6)Otro, Cual</td></tr>
<tr><td>4)Huyó</td><td>5) Se quedó quieto</td><td>6) Otro, Cuál</td><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td></td><td colspan="2">En caso de enfermendad o accidente usted consulta a:</td><td>(1)Curandero/chaman</td><td>(2)Médico</td><td>(3)Otro, Cual</td></tr>
<tr><td colspan="3">¿Alguna vez una serpiente lo ha mordido?</td><td colspan="12">1) SI / 0) NO</td></tr>
</table>

Supplement 2. Illustrative sheet with pictures of five snake species that inhabit in oil palm plantation 1) *Micrurus dumerilii*, 2) *Bothrops atrox*, 3) *Trilepida macrolepis*, 4) *Ninia atrata*, 5)*Oxyrhopus petolarius*

Supplement 3. Field tasks developed by field workers surveyed at oil palm plantation of Palmasol S.A.

General field tasks	Specific field worker tasks
Agricultural managers and technicians	Manager
	Storer
	Field assistant
	HSEQ assistant
	Kitchen assistant
	Mechanical assistant
	Mechanic
	HSEQ manager
	Chef
	Logistic technician
	Occupational health technician
Animal management and pest control	Pest controller
	Cowboy
	Animal feeder
	Animal manager
	Animal welfare
Engine drivers	Machine operator
	Tractor driver
	Driver
Fruit piker	Harvester
	Kernel collector
	Bag filler

	Fruit lifter
Multitask	Borer
	Passant
	Fertilizer
	Sower
	Fruit loader
	Preparer
	Watchman
Pollinator	Pollinator
Pruners	Scyther
	Pruner

Supplement 4. Marked and recapture snakes by sampling occasion.

Sampling period	Marked specimens	Individuals recaptured	Season	Climatic Year
aug-14	10	NA	Rainy	Good
oct-14	15	0		
nov-14	14	1		
dic-14	15	0	Dry	
jan-15	23	2		
feb-15	22	0		
mar-15	16	1		
apr-15	29	0	Rainy	
jun-15	30	1		
jul-15	21	3		
sep-15	32	4		
oct-15	29	2		
nov-15	17	0		
dic-15	30	2	Dry	
jan-16	3	0		Bad
feb-16	0	0		
mar-16	0	0		
apr-16	5	0	Rainy	
may-16	14	3		
jun-16	5	1		
jul-16	6	1		
Aug-16	8	2		
sep-16	7	0		
oct-16	3	0		
nov-16	2	0		
dic-16	6	2	Dry	
jan-17	3	0		
feb-17	0	0		
mar-17	1	0		
apr-17	6	0		
may-17	2	1	Rainy	
jun-17	4	0		

Supplement 5. Fitting competing models that examined the “best” fits with relationship between body mass and survival.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Parameters number	Deviance
{Phi(.*Mass) p(.*Mass)}	321,09	0,00	0,995	1	4	312,98
{Phi(t) p(.) }	332,38	11,29	0,00352	0,0035	8	315,98
{Phi(.) p(.*Mass)}	336,27	15,18	0,0005	0,0005	3	330,199
{Phi(.*Mass) p(.) }	336,31	15,22	0,00049	0,0005	3	330,244
{Phi(.) p(.) }	336,33	15,25	0,00049	0,0005	2	332,3017
{Phi(.) p(t*Mass) }	347,32	26,23	0	0	31	279,484
{Phi(.*Mass) p(t) }	347,59	26,51	0	0	31	279,756
{Phi(.) p(t) }	349,39	28,30	0	0	31	281,5559
{Phi (t*Mass) p (t*Mass)}	368,07	46,99	0	0	60	224,537
{Phi(t*Mass) p(.) }	370,50	49,41	0	0	31	302,663
{Phi(t) p(.*Mass) }	371,32	50,24	0	0	31	303,486
{Phi (t) p (t*Mass)}	409,30	88,22	0	0	60	265,764
{Phi (t) p (t)}	412,68	91,59	0	0	60	269,141

Supplement 6. Fitting competing models that examined the “best” fits with relationship between abiotic co-variables, sex and survival

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Parameters	QDeviance
{Phi(.) p(TH1)}	79,7056	0	0,12616	1	3	36,8354
{Phi(.) p(TH1)}2}	79,7056	0	0,12616	1	3	36,8354
{Phi (.) P (.)}	80,0721	0,3665	0,10503	0,8325	2	39,2394
{Phi(.) p(season)}	80,0726	0,367	0,10501	0,8324	3	37,2025
{Phi(.) p(TH)}	80,0991	0,3935	0,10363	0,8214	3	37,2289
{Phi(.) p(TH2)}	80,7433	1,0377	0,07509	0,5952	3	37,8732
{Phi(TH1) p(TH1)}	81,528	1,8224	0,05072	0,402	4	36,6076
{Phi(season) p(.)}	81,628	1,9224	0,04825	0,3825	3	38,7579
{Phi(TH) p(TH)}	81,9821	2,2765	0,04042	0,3204	4	37,0617
{Phi(TH2) p(.)}	82,0628	2,3572	0,03882	0,3077	3	39,1926
{Phi(TH1) p(.)}	82,1035	2,3979	0,03804	0,3015	3	39,2334
{Phi(TH) p(.)}	82,1083	2,4027	0,03795	0,3008	3	39,2381
{Phi(season) p(season)}	82,1214	2,4158	0,0377	0,2988	4	37,201
{Phi(TH2) p(TH2)}	82,7572	3,0516	0,02743	0,2174	4	37,8368
{Phi (g) P (g)}	83,845	4,1394	0,01592	0,1262	4	38,9246
{Phi(sex*TH1)	85,2796	5,574	0,00777	0,0616	6	36,2201

p(sex*TH1)}						
{Phi(sex*TH) p(sex*TH)}	85,7469	6,0413	0,00615	0,0487	6	36,6873
{Phi(g*epoca) p(g*epoca)}	85,9515	6,2459	0,00555	0,044	6	36,892
{Phi(sex*TH2) p(sex*TH2)}	86,5108	6,8052	0,0042	0,0333	6	37,4512
{Phi (sex*t) p (sex*t)}	104,5991	24,8935	0	0	22	20,4528

Supplement 7. Fitting competing models that examined the "best" fits with relationship between biotic co-variables and survival

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi (.SVL) p (.SVL)}	235,2071	0	0,57388	1	4	227,0817
{Phi (.MASS) p (.MASS)}	236,0204	0,8133	0,38214	0,6659	4	227,895
{Phi (.IBC) p (.IBC)}	241,1233	5,9162	0,02979	0,0519	4	232,9979
{Phi(g* earthworms) p(g*earthworms)}	244,1512	8,9441	0,00656	0,0114	6	231,8862
{Phi(g*total food) p(g*total food)}	246,0052	10,7981	0,00259	0,0045	6	233,7402
{Phi(g*snails) p(g*snails)}	246,0624	10,8553	0,00252	0,0044	6	233,7975
{Phi (.) p (.)}	246,4579	11,2508	0,00207	0,0036	2	242,4206
{Phi (g) p (g)}	249,5223	14,3152	0,00045	0,0008	4	241,3969
{Phi (g*t) p (g*t)}	263,6044	28,3973	0	0	31	194,8098

Supplement 8. Statistical description of *Ninia atrat*a population structure by sexes, seasons and climatic years

Weight	N	Mean	Median	Mode	Range	Standard error	Skewness	Kurtosis
Total	349	9,04	9	10	1–28.5	0,28	0,49	-0,10
Female	189	9,65	9,5	3	1–28.5	0,44	0,45	-0,54
Male	160	8,31	9	11	1–16	0,32	-0,11	-1,10
Dry season	112	7,53	7,3	1,5	1–21	0,50	0,59	-0,67
Rainy season	237	9,75	10	11	1.5–28.5	0,34	0,50	0,22
Good year	287	8,92	9	3	1–28.5	0,32	0,57	-0,10
Bad year	62	9,60	10	10	1.6–20	0,55	-0,12	-0,37

Supplement 9. Statistical description of *Ninia atrat*a population structure by sexes, seasons and climatic years

Scenario	Snake killing rate/year	Snake added or subtracted	λ	Damping ratio
Current situation	192	0	0.895	1
No snake-killing scenario	0	192	0.895	1
Intensive snake-killing	288	-288	0.895	1
Population size increases scenario	0	288	0.895	1
Lynch et al (2014)	364	-364	0.895	1

Supplement 10. Script for R environment that developed the Integral Projection Models employed as demographic approach to test the hypothesis that intentional snake killing by peasants and field workers represents a significant threat for snake conservation (Lynch, 2012).

```
### Body mass as descriptive variable of IPM. Script version 28_09_2017 developed by Teddy
### Angarita-Sierra and Hibraím A. Pérez-Mendoza
### Script based on appendices of “Advancing population ecology with integral projection models:
### a practical guide (Merow et al 2014, Methods in Ecology and Evolution )
```

1.**Load packages**

```
require(IPMpack)
require(popdemo)
require(viridis)
```

2. Load data

```
datosIPM<-Datos_IPM_MASA_Final(15_08_2017).csv",header=TRUE,encoding="latin1")
dataparametros<-Parametros_Ninia_Masa(FINAL_28_09_2017).csv",header=TRUE,encoding="latin1")
```

3. Rename data

```
d=datosIPM
pp=dataparametros
```

4. Data frame building

```
params=data.frame(
surv.int=NA,
surv.slope=NA,
growth.int=NA,
growth.slope=NA,
growth.sd=NA,
newb.int=NA,
newb.slope=NA,
recruit.size.mean=NA,
recruit.size.sd=NA)
```

5. Build regressions for vital rate functions

```
###      a) Apparent survival function(Logistic regression)

surv.reg=glm(Survival~T0,data=d,family=binomial())
summary(surv.reg)

### Filling data frame built
params$surv.int=pp[1,1]
params$surv.slope=pp[1,2]

###      b) Growth function (lineal regression )

growth.reg=lm(T1~T0,data=d)
summary(growth.reg)
```

```
### Filling data frame built
params$growth.int=pp[1,3]
params$growth.slope=pp[1,4]
params$growth.sd=pp[1,5]

###     c) Fecundity function. Relationship between female body mass and clutch size

Fec.reg=glm(Fecundity~T0,data=d,family=poisson())
summary(Fec.reg)

### Filling data frame built
params$newb.int=pp[1,6]
params$newb.slope=pp[1,7]

 ###    d) Recruits size distribution observed
### Filling data frame built
params$recruit.size.max=max(d$T1[is.na(d$T0)])
params$recruit.size.min=min(d$T1[is.na(d$T0)])

### 6. Define functions to describe demographic processes
###     a) Apparent survival probability function

s.x=function(x,params) {
u=exp(params$surv.int+params$surv.slope*x)
return(u/(1+u))
}

###     b) Growth function

g.yx=function(xp,x,params) {
dnorm(xp,mean=params$growth.int+params$growth.slope*x,sd=params$growth.sd)
}

###     c) Reproductive function. It is defined as the interaction between the relationship between
###       female body mass and clutch size, and the recruit

f.yx=function(xp,x,params) {
dunif(xp,max=params$recruit.size.max,min=params$recruit.size.min)*
exp(params$newb.int+params$newb.slope*x)
}

### 7. Defining the integral function limits and dimensions
### Limits of the integral function. These must be expanded a little from its real values

min.size=.9*min(c(d$T0,d$T1),na.rm=T)
max.size=1.1*max(c(d$T0,d$T1),na.rm=T)

### Number of grids in the kernel

n=100
```

```
### Limits of the kernel´s grid
b=min.size+c(0:n)*(max.size-min.size)/n

### Definition of mesh point

y=0.5*(b[1:n]+b[2:(n+1)])

### Grid´s width

h=y[2]-y[1]

### 8. Building the Kernels
###	a) Growth kernel

G=h*outer(y,y,g.yx,params=params)

###	b) Suvival

S=s.x(y,params=params)

###	c) Placeholder; we're about to redefine P on the next line

P=G

for(i in 1:n) P[,i]=G[,i]*S[i]

###	d) Reproductive kernel

F=h*outer(y,y,f.yx,params=params)

### 9. IPM Matrix or Full Kernel

K=P+F

###	a) Output file of the IPM matrix

write.csv2(x=K, file="Kernel.csv", row.names=FALSE, na="")

### 11.Basic asymptotic analyses

###	a) Dominant eigenvalue λ that represents the population's asymptotic growth rate

lam1=Re(eigen(K)$values[1])
lam1

###	b) Dominant right eigenvector or stable mass distribution

w.eigen=Re(eigen(K)$vectors[,1])
stable.dist=w.eigen/sum(w.eigen)


###	c) Dominant left eigenvector or mass-specific reproductive value
```

```
v.eigen=Re(eigen(t(K))$vectors[,1])
repro.val=v.eigen/v.eigen[1]
```

12. Sensitivity and elasticity analyses

```
v.dot.w=sum(stable.dist*repro.val)*h
sens=outer(repro.val,stable.dist)/v.dot.w
summary(sens)
elas=matrix(as.vector(sens)*as.vector(K)/lam1,nrow=n)
summary(elas)
```

###13. Plot these results (stable size distribution, reproductive values, elasticity, sensitivity).

```
par(mfrow=c(2,3), mar=c(4,5,2,2))
image(y,y,t(K), xlab="Size (t)",ylab="Size (t+1)",col=inferno(256), main="IPM matrix")
contour(y,y,t(K), add = TRUE, drawlabels = FALSE)
plot(y,stable.dist,xlab="Size",type="l",main="Stable size distribution")
plot(y,repro.val,xlab="Size",type="l",main="Reproductive values")
image(y,y,t(elas),xlab="Size (t)",ylab="Size (t+1)", col= inferno(256), main="Elasticity")
image(y,y,t(sens),xlab="Size (t)",ylab="Size (t+1)", col= inferno(256), main="Sensitivity")
```