



Universidade Estadual da Santa Cruz
Programa de Pós Graduação em Ecologia e Conservação da
Biodiversidade

ECOLOGIA DO MOVIMENTO EM SERPENTES: UMA
ABORDAGEM MACROECOLÓGICA DAS CAUSAS E
CONSEQUÊNCIAS POR TRÁS DESTE COMPORxTAMENTO

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**ECOLOGIA DO MOVIMENTO EM SERPENTES: UMA
ABORDAGEM MACROECOLÓGICA DAS CAUSAS E
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Resumo

Movimento é a mudança na posição espaço-temporal de um indivíduo. Ele sofre influência de fatores externos do ambiente e de internos, oriundos de dentro do corpo do indivíduo. Uma de suas consequências diretas é o uso do espaço, pois o próprio conceito de movimento necessita de posições espaciais conhecidas para ser definido. A maneira mais comum de se medir uso do espaço é pela análise de área de vida, o espaço usado por um indivíduo durante um período de tempo. Pesquisas sobre o movimento e área de vida dos seres vivos tem se tornado cada vez mais comuns na última década, especialmente na ecologia do movimento com ênfase no movimento dos animais, como consequência, uma quantidade nunca vista antes de dados sobre movimento está disponível nas plataformas online. O presente trabalho fez um levantamento bibliográfico sobre estudos de ecologia do movimento em serpentes no intuito de sumarizar o conhecimento disponível na literatura e comparar os artigos para ajudar a esclarecer contradições e encontrar conclusões mais precisas. A grande maioria dos trabalhos seguem as mesmas metodologias, investigando a relação do movimento com alguma variável sem aprofundar a discussão para as repercussões ecológicas. Os trabalhos estão mais concentrados na região da América do Norte principalmente nos Estados Unidos da América (EUA) com algumas poucas espécies da família Viperidae e Colubridae sendo muito estudadas enquanto a grande maioria das espécies aparece em poucos artigos. A influência de fatores externos e internos no movimento e uso do espaço é bem estudada, no entanto poucos artigos estudaram capacidade locomotora e capacidade de navegação, ainda menos estudaram a relação do movimento com a sobrevivência, sucesso reprodutivo, competição intra e interespecífica e sua influência na dinâmica da população, comunidade e ecossistema. O movimento das serpentes não é aleatório, serpentes se locomovem de maneira a conseguir os recursos necessários a manutenção de sua vida e evitar condições potencialmente perigosas. Também acompanham as variações sazonais na disponibilidade de recursos e mantem sua área de vida em volta de abrigos. Abrigos de boa qualidade são usados novamente e em alguns casos compartilhados com outras serpentes, outras espécies de répteis e até anfíbios. Os padrões de movimento e uso de espaço das serpentes, não sofrem grande influência das relações filogenéticas, mas por características individuais utilizando parâmetros como tamanho, sexo, idade, bem como período reprodutivo, e por características comuns as espécies como modo reprodutivo, período de atividade e tipo de micro ambiente ocupado.

Abstract

Motion is the change in an individual's space-time position. It is influenced by external factors of the environment and internal ones, coming from inside the individual's body. One of its direct consequences is the use of space, since the very concept of movement needs known spatial positions to be defined. The most common way to measure space use is by analyzing home range, the space used by an individual over a period of time. Research on the movement and home range of living beings has become increasingly common in the last decade, especially in the ecology of movement with an emphasis on the movement of animals, as a consequence, a never seen before amount of data on movement is available on online platforms. The present work carried out a bibliographic survey on studies of ecology of movement in snakes in order to summarize the knowledge available in the literature and compare the articles to help clarify contradictions and find more accurate conclusions. The vast majority of works follow the same methodologies, investigating the relationship of movement with some variable without deepening the discussion of ecological repercussions. The works are more concentrated in the North American region, mainly in the United States of America (USA) with a few species of the Viperidae and Colubridae family being very studied while the vast majority of species appear in few articles. The influence of external and internal factors on movement and use of space is well studied, however few articles have studied locomotor ability and navigation ability, even fewer have studied the relationship of movement with survival, reproductive success, intra and interspecific competition and its influence in population, community and ecosystem dynamics. The movement of snakes is not random, snakes move in order to get the necessary resources to maintain their lives and avoid potentially dangerous conditions. They also track seasonal variations in resource availability and maintain their home range around roosts. Good quality shelters are reused and in some cases shared with other snakes, other species of reptiles and even amphibians. The patterns of movement and space use of snakes are not greatly influenced by phylogenetic relationships, but by individual characteristics using parameters such as size, sex, age, as well as reproductive period, and by characteristics common to species such as reproductive mode , period of activity and type of microenvironment occupied.

Introdução Geral

O movimento é um comportamento indispensável para um ser vivo realizar as atividades necessárias a manutenção de sua vida (Nathan, 2008A). Deste modo, ele pode ser definido como a mudança na posição espacial de um indivíduo ao longo do tempo (Nathan, 2008 A). Todos os organismos, mesmo os unicelulares ou de natureza sésil se locomovem em algum momento de sua vida em alguma escala espacial. Este movimento pode ocorrer de maneira autônoma, carregados por outros organismos ou por fatores abióticos do ambiente onde vivem, o que faz do movimento um comportamento comum a todos os seres vivos (Nathan, 2008 B; Holyoak, 2008). Desta forma, entender o movimento dos organismos nos ajuda a compreender mais sobre como os seres vivos percebem, interpretam e interagem com o ambiente a sua volta (Holyoak, 2008; Brum-Bastos, 2022).

O movimento de um organismo pode derivar tanto de fatores externos, advindos do ambiente ao seu redor, como mudanças de temperatura (Signore, 2022), de clima (Quintana, 2017), de terreno, entre outras (Nathan, 2008). Este comportamento também pode ser influenciado pela interação com outros organismos, tais como presença de predadores ou competidores (Kjoss, 2001; Nathan, 2008); como também de fatores internos, estímulos oriundos de dentro do corpo do indivíduo, como a necessidade de se alimentar ou beber água (Crysti, 2017), instintos migratórios (Bridge, 2011), busca por conforto (Hand, 2019), entre outros (Nathan, 2008).

Uma das consequências diretas do movimento é o uso do espaço, uma vez que o próprio conceito de movimento necessita de posições conhecidas do indivíduo no espaço onde vive para ser definido. O uso do espaço pode ser medido de várias maneiras, a mais comum é pela análise de área de vida, refletindo o espaço usado por um indivíduo durante um período de tempo (Powell e Michell, 2012). O comportamento de área de vida, também conhecida como área de uso, resulta de um processo de tomada de decisão que visa melhor aproveitar os recursos espacialmente distribuídos no ambiente,

portanto, pode se afirmar que trata-se de um reflexo do entendimento do indivíduo sobre o ambiente que o circunda (Michell e Powell, 2012; Powell e Michel 2012).

Pesquisas sobre o movimento e área de vida dos seres vivos tem se tornado cada vez mais comuns na última década, especialmente na ecologia do movimento com ênfase em animais, o que se deve em parte ao avanço e barateamento das tecnologias de rastreamento e monitoramento que permitem uma coleta de dados mais abrangente e precisa (Demšar et al.,2021). Como consequência, uma quantidade nunca vista antes de dados sobre movimento está disponível nas plataformas online, a ecologia do movimento tem se aproveitado destes bancos de dados para estudar as variações do movimento e uso de espaço entre indivíduos e espécies, bem como respostas comportamentais ao ambiente através de uma larga escala espacial e temporal (Nathan, 2022). Neste contexto a ecologia do movimento tem expandido suas fronteiras para cenários interdisciplinares e colaborativos gerando novas descobertas não só sobre movimento e uso de espaço, mas também sobre suas causas e consequências para conservação das espécies dos mais diferentes grupos em ecossistemas ao redor do mundo (Fraser, 2018; Jacoby, 2016; Williams, 2020;Nathan, 2022).

Serpentes são répteis da ordem Squamata que ocorrem em baixa densidade e podem permanecer escondidos em abrigos por semanas ou até meses, por isto tem sido pouco abordadas em trabalhos ecológicos (Mullin e Seigel, 2009). Apesar disso, apresentam uma grande plasticidade em relação a diversas características ecológicas e de história de vida, tornando-as modelos interessantes para estudos ecológicos (Shine e Bonnet, 2000). Apesar disso, o conhecimento sobre suas características ecológicas é pobre e assistemático, mesmo informações básicas sobre história natural e distribuição são escassas para muitas espécies (Roll et al., 2017; Cox, et al 2022). Visto que serpentes são um grupo de vertebrados amplamente difundido em todo o mundo, esta é uma grande lacuna no conhecimento da biodiversidade moderna (Shine and Bonnet, 2000; Mullin e Seigel, 2009; Roll et al.,2017).

Estudos anteriores mostram que o movimento e a área de vida das serpentes são afetados por vários fatores ambientais e morfológicos, como temperatura (Eskew e Todd, 2017), umidade (Costanzo, 1989; Daltry et al., 1998), incidência de luz lunar (Brown e Shine, 2002), latitude (Benhamou e Riotte-Lambert, 2012), sexo (Brown e Shine, 2002; Hyslop et al., 2014), idade (Brown e Shine, 2002), modo reprodutivo (Lourenço-de-Moraes et al., 2019), etc. Tais estudos têm encontrado resultados contraditórios para diferentes populações e espécies. Por exemplo Reinert (1988), de Gregorio (2011) e Petersen (2019) viram que serpentes machos se locomovem mais que as fêmeas, no entanto, Shine (1987) e Carrasco-Harris (2020) afirmam que fêmeas geralmente se locomovem mais. Em outra vertente, Blazkes (1995), Karns (1999) e Michael (2013) afirmam ainda que o movimento não é afetado pelo sexo das serpentes.

O mesmo tipo de variação ocorre com os estudos sobre área de vida em serpentes. Sabe-se que o tamanho da área de vida de uma serpente pode variar de acordo com a espécie (Dugan, 2016), sexo (de Gregorio, 2011), gravidez (Blouin-Demers, 2007), estação do ano (Quintana, 2017), abundância de presas (Crysti, 2017), tamanho corporal (Hyslop, 2014), competição interespecífica (Kjoss, 2001), estrutura da paisagem (Hoss, 2010), localização de recursos (Baxley, 2009), fragmentação de habitat (Anguiano, 2015), e até entre indivíduos da mesma espécie em diferentes regiões geográficas (Mead e Stark, 2018). A contradição persiste se abordamos os estudos com área de vida, por exemplo enquanto Buchanan (2017), Ettling (2013), Howze (2015) e de la Quintana (2017) afirmam que o tamanho da área de vida de uma serpente não é afetado pelo sexo do indivíduo, Adams (2005) e Leuemberger (2019) afirmam que a área de vida das fêmeas é maior que a dos machos. Ao mesmo tempo que Angelici (2000), Bauder (2019) Brown e Whitehead (1999) e de Gregorio (2011) afirmam que machos apresentam áreas de vida com tamanho superior ao das fêmeas.

Dada a quantidade de trabalhos existentes sobre o movimento e área de vida das serpentes, feitos em diferentes regiões do planeta e com diferentes

espécies e que chegaram a diferentes conclusões utilizando uma metodologia similar, é difícil concluir alguma coisa observando estes estudos separadamente. Deste modo, a reunião e sumarização e comparação destes dados se faz necessária para esclarecer estas ambiguidades entre os resultados dos papers de modo a identificar as causas destas variações ambíguas e nos levar a conclusões mais coesas. O presente estudo visa reunir todo o conhecimento disponível na literatura científica sobre o movimento e a área de vida das serpentes, em todo o mundo, assim como identificar os fatores ecológicos e morfológicos que influenciam esses comportamentos.

A tese está dividida em dois capítulos, no primeiro, intitulado fizemos uma permanova testando a relação de diversas variáveis através dos dados obtidos nos trabalhos encontrados na revisão, no segundo discutimos a fundo as conclusões dos artigos agrupamos e comparamos o conhecimento contido neles para tirar conclusões mais precisas.

Cap 1: Medeiros, W.S.; Morais, M.; Grundmann, D. N.; Lourenço-de-Morais,R.; Rodrigues-França,F.G.; Solé, M.K..The Influence Of Functional And Phylogenetic Traits On Snakes Movement And Home Range . Submetido Ao Journal Of Ecology and evolution

Cap 2: Medeiros, W.S.; Rodrigues França,F.G.; Solé M.K.. The Science Behind Snake Slither: What Do We Know So Far About Snakes Movement Ecology. Submetido ao journal of biogeography

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**CAPITULO 1: THE INFLUENCE OF
FUNCTIONAL AND PHYLOGENETIC
TRAITS ON SNAKES MOVEMENT AND
HOME RANGE**

THE INFLUENCE OF FUNCTIONAL AND PHYLOGENETIC TRAITS ON SNAKES MOVEMENT AND HOME RANGE

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ABSTRACT

Combining individual movement and home range data can allow us to better understand how an animal interacts with its surroundings and how this influences ecological dynamics. Previous studies about the movement and home range of snakes have shown several factors influencing them. Usually, these studies were made with different species, methods and regions, hampering a comparative analysis to identify general patterns. The present study aims to review all available literature about snake movement and home range identifying the influence of phylogenetic, ecological, and morphological

factors on these behaviors. We conducted an exhaustive survey of specialized journals and online databases for papers that used radio telemetry to track snakes. We found 448 papers and after applying the filter selected 86 of them. Our results show that movement and home range have no phylogenetic signal, however, functional traits are linked to snake's habits and reflect the particularities of survival strategies and morphologies of each group. Larger and heavier snakes move more and occupy larger areas. Snake movement seems to be more efficient in aquatic environments. We expect that these conclusions help us to understand the snake behaviour and its relation with their environment, what can be used in conservation projects.

Keywords: Behavior, Biogeography, Evolution, Spatial Ecology

INTRODUCTION

Movement is defined as a change in the spatial position of an organism through time (Nathan et al.,2009). It is a fundamental feature of living creatures on earth, playing a deterministic role in several aspects of their life history (e.g. survival, reproduction, and mating) (Nathan et al.,2009). Several studies have quantified the movement of different species and technological advances have made it possible to track more individuals, producing more detailed spatiotemporal data on mobile animals and allowing large-scale analysis of movement and space use patterns in a macroecological approach (Fraser et al.,2018; Holyoak et al.,2008; Nathan et al.,2008).

Space use is one of the consequences of animal movement and is commonly measured by home range analysis, reflecting the space used by an individual over determined period (Powell and Michell, 2012). A home range behavior results from a decision-making process shaped by natural selection to better exploit the spatially distributed resources in the environment, and therefore represents an interplay between the environment and the animal's perception of it (Powell and Michell, 2012). The study of space use and movement patterns combined allows us to understand better how an organism

understands and interact with the environment that surround it (Hawkes, 2009; Jonsson et al., 2016).

Functional traits are species' physiological, morphological, or life history characteristics (Petchey, 2006). Snakes show remarkable plasticity regarding several functional traits, turning them into interesting models for ecological studies (Shine and Bonnet, 2000). Different functional traits (e.g. reproductive modes) can provide different distribution patterns in response to environmental changes (Lourenço-de-Moraes et al.,2019). Despite this, the knowledge about their functional traits is still poor and unsystematic, even basic information about natural history and distribution is missing for many species (Roll et al.,2017), this can be considered as one large gap in biodiversity knowledge (Shine and Bonnet, 2000; Mullin and Seigel, 2009; Roll et al.,2017).

Previous studies about movement and home range of snakes have shown several factors influencing these traits (e.g.: Hinderliter and Lee, 2004; Adams, 2005; Buchanan, 2017; Plumer, 2020). Usually, these studies were made with other species, using other methods and in different regions hampering a comparative analysis of the results to identify general patterns. The present study aims to review all available literature about snake movement and home range and identify the influence of phylogenetic and functional traits. Our central hypothesis is that snake home range size and average daily movement are influenced more strongly by ecological and functional traits than by phylogeny, and thus will be more closely correlated with species-specific functional traits than with phylogenetic patterns of relatedness.

METHODS

We systematically searched for papers that tracked snakes with radio telemetry in the Google Scholar, Core, Jstor, and BioOne platforms; in the online content of Journal of Herpetology, Acta Herpetologica, Copeia, Amphibia-Reptilia, and Herpetozoa, and all issues of the Herpetological Review and Salamandra - German Journal of Herpetology. We used the search terms: “snake” AND “movement” OR “home range” AND “telemetry”. For the studies that monitored the same individual in different years, we used only data from the first year, assuming that this would be the year with less influence of the researcher on snake behavior. From studies with manipulated conditions, we used only data from the control group.

We excluded papers that forced-feed the transmitters on snakes, because this method can injure the animal and consequently change their natural behaviour(Weatherhead, 1984). We also excluded papers that used captivity animals and manipulated field conditions, because they not reflect the behaviour of wild snakes in their natural environment

We included in the database all papers that used radio telemetry to track snakes and gathered the following information from each monitored individual: daily movement (total distance moved divided by the monitoring time) and home range area (calculated with minimal convex polygon method). The species taxonomy was revised and updated according to the Reptile Database (<http://www.reptile-database.org/>) and the species classified by family (according to Zaher et al.,2019 and minor issues as authors cited in apendix 4 in supplementary material). The functional traits were: sex, SVL (Snout-vent length, mean value for all individuals of each species in the database, in mm), body mass (mean value for all individuals of each species in the database in gram) and reproductive mode (viviparous, oviparous, and ovoviviparous). The ecological traits are activity (diurnal or nocturnal), habit (fossorial, arboreal, aquatic, semi-aquatic, and terrestrial) and habitat (closed -where the trees' canopy forms a barrier to light and humidity, open -where the barrier does not

occur, and semi-open -a matrix of both kinds of environments where the animal can access both).

In cases of missing data, gaps were filled with the average of values from all individuals of the same sex and species already in the database, and when this was not possible, we used values of the phylogenetically closest species as possible (see appendix 3 in the supplementary material for more details). Only when the gaps could not be filled, we excluded these individuals from our database. For each snake family, we performed two PERMANOVA analysis in the R environment version 4.0.0, one with home range and a nother with average daily movement as response variables and SVL, taxonomic family, the country where the study was made, locomotory habit, mass, sex, activity period, and reproductive mode as well all their possible interactions as predictors (adapted of Oksanen, 2007).

Phylogenetic signal

The phylogenetic signal is often defined as a tendency of closely related species to resemble each other about their phenotypes more than if compared to other random species (Harvey and Pagel, 1991; Blomberg and Garland, 2002). To quantify the phylogenetic signal in the mean daily movement and home range, we initially pruned a fully-sampled global phylogeny of Squamata (Tonini et al.,2016) to include only the species in our dataset. We measured the phylogenetic signal in the mean daily movement and home range, using Abouheif's test (Abouhef, 1999) and Blomberg's *K*-statistic (Blomberg et al.,2003). The Abouheif's test is based both on Moran's I and Geary's c tests (Legendre and Fortin, 1989). Values closer to zero indicate the absence of a phylogenetic signal. We used the Abouheif's test implemented in the "adephylo" package(phylosig command) with 1000 randomizations (Pavoine et al.,2008) in the R software 4.0.0 (R Core Team, 2020).

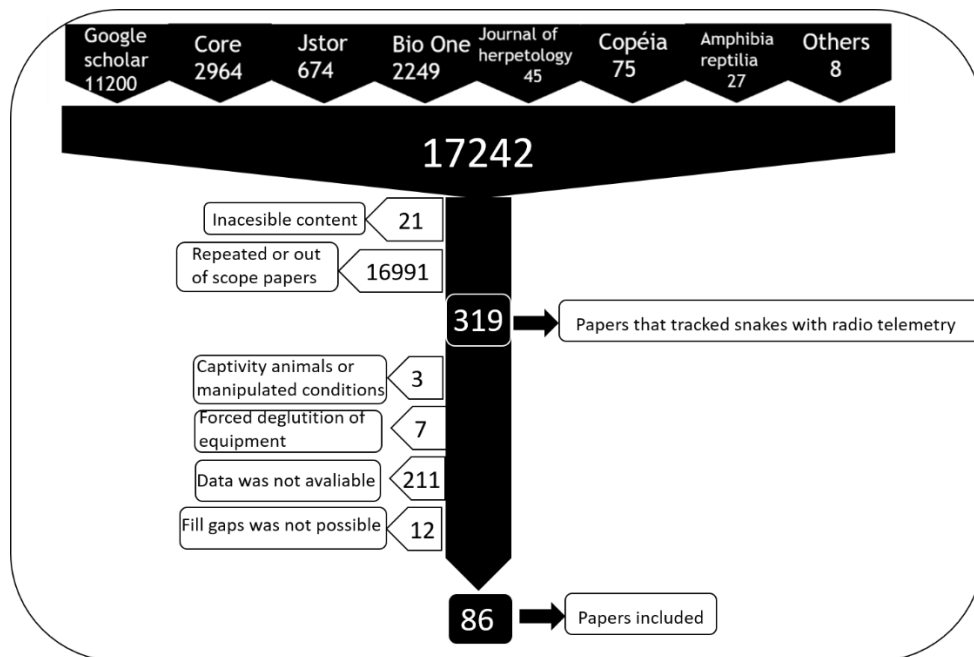
Blomberg's *K*-statistic is the ratio between the observed variation in trait values and the variation expected under a Brownian-Motion (BM) model of trait evolution. *K* values < 1 indicate lack of phylogenetic signal whereas *K* > 1 indicates more phylogenetic signal than expected under BM. The significance of *K* was assessed through randomization tests that produced a null distribution of

1000 *K* values using the ‘phytools’ package (Revell, 2012) in R software 4.0.0 (R Core Team 2020). For the reconstruction of the trait in phylogeny, we used the functions ‘contMap’ using the ‘phytools’ package (Revell, 2012).

RESULTS

We found 319 papers and select a total of 84 studies from them including papers published in journals, unpublished dissertations, thesis, and technical reports (Figure 1, for more details see appendix 2 in supplementary material). We built a database with all individuals with available data. The database included a total of 1010 individual snakes belonging to 48 species and 9 families.

Figure 1: Criteria for selection of papers and exclusion filters.



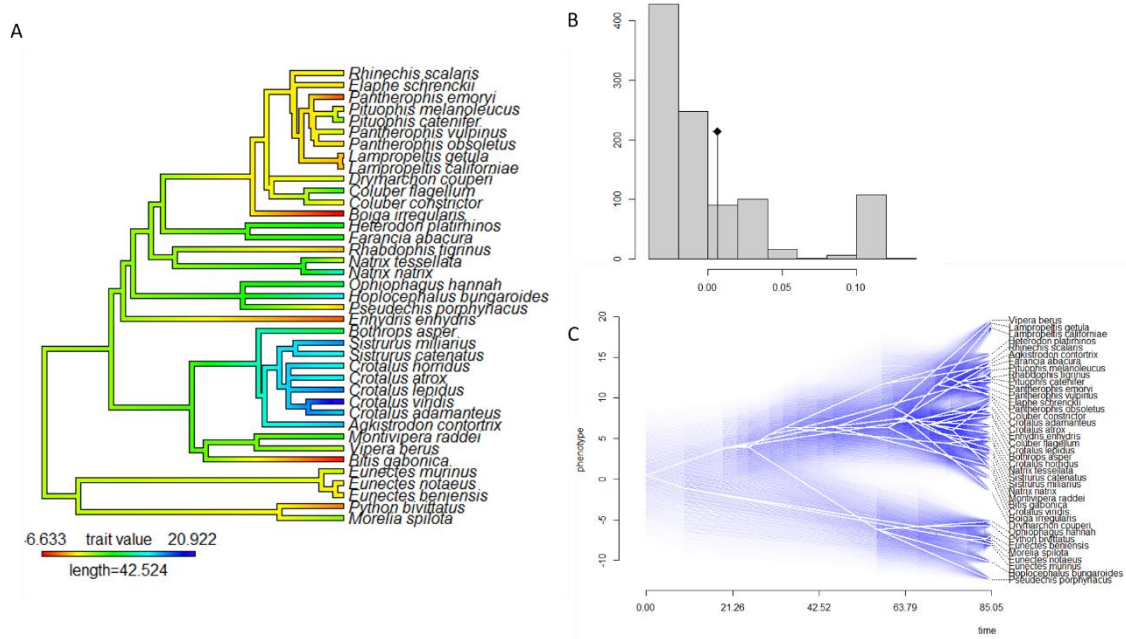
In PERMANOVA analysis with mean daily movement as response variable showed different weights of influence of the tested parameters among the different snake families. For Boidae, the most influent variable was aquatic environment ($r^2=0.060$; $P<0.001$), for Colubridae, was open environments ($r^2=0.380$; $P<0.001$), for Elapidae was Body size (SVL, $r^2=0.250$; $P<0.001$), for Homalopsidae was female sex ($r^2=0.250$; $P<0.001$), for Viperidae was diurnal

habit ($r^2=0.230$; $P<0.001$) and for Acrochordidae, Dipsadidae and Pythonidae, no significant influence of variables were observed (see appendix 1, table 1 in supplementary material) .

In PERMANOVA analysis with home range as response variable, the best-fitted value was oviparous for Elapidae ($r^2=0.440$; $P<0.001$) followed by habitat open for Colubridae ($r^2=0.380$; $P<0.001$) (see appendix 1 in supplementary material). We found no significant interactions for the snake families Acrochordidae, Dipsadidae, and Pythonidae in the variables with significant influence on the home range size of snakes from the dataset. The best-fitted value was SVL for Elapidae ($r^2=0.490$; $P<0.001$) followed by mass for Boidae ($r^2=0.3800$; $P<0.006$) (see appendix 1, table 2 in supplementary material). We found no significant interactions for the families Natricidae, Dipsadidae, and Homalopsidae.

General phylogenetic signal was not detected for home range (Table 1 and Figure 2) or mean daily movement (Table 1 and Figure 3). Both characteristics had recent origins in these groups (Figures 2, 3). The tracking of traits in the tree shows that the home range has a strong relationship between the species of Viperidae (Figures 2), and the mean daily movement has a strong relationship between Colubridae (Figures 3).

Figure 2: Phylogenetic signal for home range. A) strength of the signal for each taxon; B) About's authorization histogram; C) Origin of the signal in the tree.



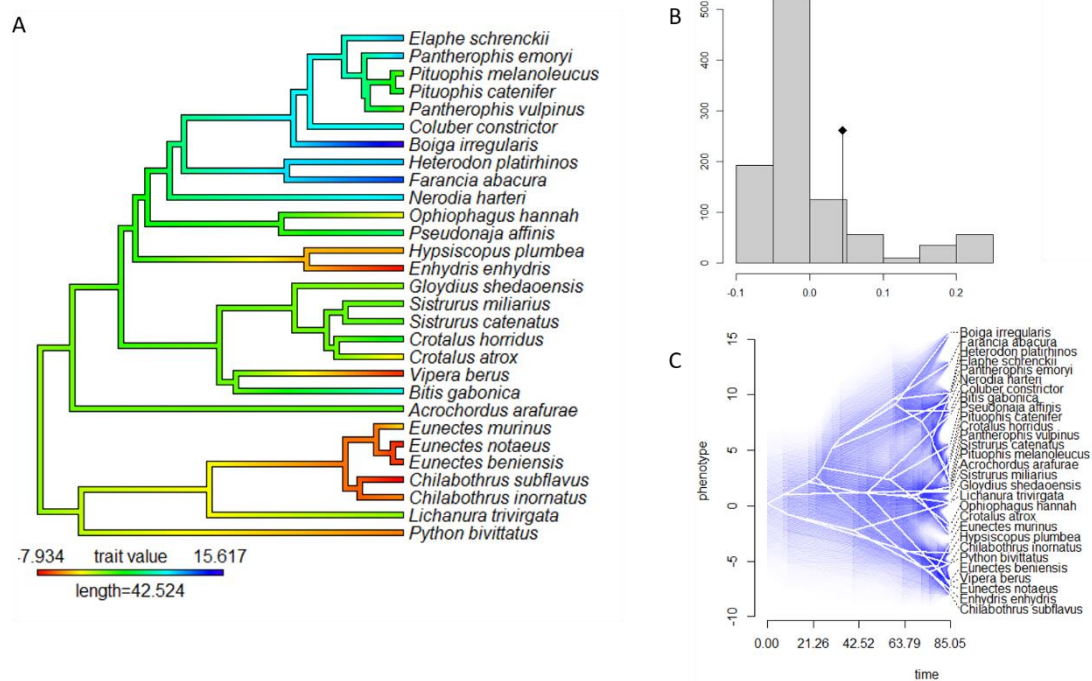


Figure 3: Phylogenetic signal for movement. A) strength of the signal for each taxon; B) Abouf's authorization histogram; C) Origin of the signal in the tree.

Table 1 Phylogenetic signal values for home range and average daily movement

	Test	Value	P value
Home range	Abouheif's test	0.006258871	0.245
	Blomberg's statistic	K- 0.386781	0.35035
Average daily movement	Abouheif's test	0.04517163	0.161
	Blomberg's statistic	K- 0.48264	0.318318

DISCUSSION

Our results show that the factors influencing movement and home range are different for each snake family. For all snake families, length and body mass are influential factors regarding home range and average daily movement, probably due to the mortality rate of snakes in the wild being inversely proportional to their size. Thus, a big snake faces less danger when moving large distances and exploring new areas (Bonnet et al., 1999; Shine et al., 2001). In addition, ovoviviparous and oviparous snakes tend to move more than viviparous. During pregnancy, viviparous snakes have a reduction in their food intake rate, locomotory performance, activity, survival rate, and an increase in thermoregulation time, secretive behavior, and metabolic costs for at least three months (Shine, 2006; Blackburn 2011).

In Boidae, aquatic species move more than terrestrial ones. The undulatory locomotion used by snakes to move in both aquatic and terrestrial environments results in more body undulations in the water than on land with the same strength applied (Gillis and Blob, 2001; Gray, 1951; Jayne, 1988). More undulation frequency implies more track points and consequently increased movement speed, thus snake movement is more efficient in terms of cost-benefit in the water than on land (Gillis and Blob, 2001; Gray, 1951; Jayne, 1988).

For Colubridae, we found a strong relation of trait daily movement. Also, diurnal snakes tended to move more. Snakes have an activity rate dependent on habitat heat (Brown and Shine, 2002; Dmi'el, 1972; Eskew and Todd, 2017; Heckrotte, 1967), a resource more abundant during daytime, this trait seems to be specially strong in this family. We found that colubrids that living in the habitat of open or closed areas tended to move more than those living in semi-open areas. This can be due species from enclosed areas need access to open areas to thermoregulate and species from open areas need to move to closed areas to escape excessive heat (Abney, 2019; Lelièvre et al., 2011). However, mixed-area species don't need to do any of that because the next sunny spot is close to the next shady spot, therefore they have to move less. Males tend to

move more than females, which can be explained by males of this family searching for females during the mating season (Hyslop et al.,2014).

In Elapidae, males tend to move more and have larger home ranges than females, suggesting that they search for females during reproduction period. On the other hand, Colubridae species explore new areas to find potential partners. Information about Elapidae courtship behavior is scarce. Broadley and Baldwin (2006) reported field observations of male combat in the genus *Aspidelps* and Shine (1981) reported the same behavior in *Pseudechis porphyriacus*. The SVL influences the movement of semi-aquatic elapids suggesting that body length is equally influenced by aquatic and terrestrial habits. Oviparous elapids have a better fit than other reproductive modes and this is because almost all elapid species included in our analysis are oviparous, thus reflecting sample number.

In Homalopsidae, females tend to move more than males. Reproduction demands high energetic costs of females' bodies (Shine, 2003). To compensate for these costs some snake species increase their food intake rate when pregnant (Murphy, 2007; Schuett et al.,2013). Since this behavior is present in the homalopsid snakes, they are specialized in small prey and live in tropical waters where the digestion is faster, which can compel the female to move to search for food more frequently (Murphy, 2007).

In Pythonidae, arboreal snakes tend to have larger home ranges. The movement in arboreal environments is more costly than in terrestrial, however, it is safer since the risk of being spotted is lower (Byrnes and Jayne, 2014). This also can be due to arboreal snakes frequently opting for a less inclined route instead of going straight, which generates more irregular trajectories and increases the distance from the core area in several points and consequently their home range area (Byrnes and Jayne, 2014).

For the Viperidae family, we found a strong phylogenetic signal for the home range. Diurnal viperids tend to move more than nocturnal, a result like that found for Colubridae. This tendency is especially strong for females. However, the opposite occurs about the home range, nocturnal snakes having larger home ranges. This tendency also is stronger for females. It suggests that

diurnal viperids are more active and possibly more territorial, moving frequently around the same area while the nocturnal species tend to be more sedentary but are more propense to explore new areas. This can be due the use of sit-and-wait hunting strategy for nocturnal viperids, that the diet is composed primarily for small mammals that are active during the night. Females moving more than males can be a reflection of SVL effect because, in some species of viperid snakes, females are larger than males (Maritz and Alexander, 2011; Shine, 1978). Oviparous viperids tend to move more, this can be due to the lack of the extra height that the embryos represent by depositing the eggs, while viviparous species have to carry the embryos until they are fully developed and born. Viviparous viperids also show larger home ranges than oviparous species, which suggest an inclination to move to new areas, possibly to avoid competition with the newborn (Shine, 2006; Blackburn, 2011).

CONCLUSION

The movement and home range of snakes are influenced by several environmental and physiologic variables according to the snake group. Although phylogenetic signal was not significant for all species in this dataset, was strong among viperidae, so we can assume that phylogeny is not the main driver of these behaviors, however they have some influence. Also, The origin of phylogenetic signal of movement and home range is more recent than the separation of the snake groups, thus the environment seems to be the main driver of these characteristics. Movement and space use are more likely driven by needs of the individual life of the snakes according to the conditions imposed by their environment and the strategies utilized to transpose them to realize their regular activities (like feed, rest, mate, and others).

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Appendix 1 - Tables

Table 2: Fit values of variables with significant influence on the average daily movement of each snake family.

Variable	r ²	p
Acrochordidae	no significant interations	
Residuals	0.900	
Boidae		
Aquatic	0.350	0.001
Svl	0.060	0.030
Residuals	0.460	
Colubridae		
Diurnal	0.010	0.010
Male	0.004	0.009
Mass	0.070	0.001
Closed enviroments	0.090	0.001
Open enviroments	0.380	0.001
Svl*Mass	0.020	0.002
Svl*Open	0.360	0.001
Residuals	0.030	
Dipsadidae	no significant interations	
Residuals	0.770	
Elapidae		
Oviparous	0.440	0.001
Male	0.040	0.009
Svl	0.250	0.001
Closed	0.010	0.040
Semi-aquatic*Svl	0.090	0.004

Oviparous*Mas	0.110	0.006
Residuals	0.005	
Homalopsidae		
Female	0.250	0.020
Svl	0.190	0.030
Residuals	0.280	
Pythonidae		
	no significant interations	
Residuals	0.990	
Viperidae		
Diurnal	0.230	0.001
Ovoviviparous	0.010	0.010
Mass	0.070	0.001
Ovoviviparous*Diurnal	0.060	0.001
Diurnal*Svl	0.050	0.002
Diurnal*Mass*Female	0.030	0.007
Residuals	0.460	

Table 3: Fit values of variables with significant influence on home range of each snake family.

Variable	r^2	p
Natricidae		
	no significant interations	
Residuals	0.540	
Boidae		
Mass	0.380	0.006
Svl*Mass	0.140	0.020
Residuals	0.290	
Colubridae		
Mass	0.080	0.001

Closed environments	0.020	0.010
Svl*Open environments	0.020	0.010
Residuals	0.810	
Dipsadidae		no significant interactions
Residuals	0.780	
Elapidae		
Noturnal	0.020	0.010
Male	0.020	0.005
Svl	0.490	0.001
Mass	0.020	0.040
Closed environments	0.120	0.001
Male*Svl	0.040	0.020
Residuals	0.230	
Homalopsidae		no significant interactions
Residuals	0.850	
Pythonidae		
Arboreal	0.150	0.009
Svl	0.150	0.020
Residuals	0.560	
Viperidae		
Noturnal	0.010	0.060
Noturnal*Female	0.040	0.040
Noturnal*Svl	0.050	0.030
Noturnal*Viviparous*Female	0.070	0.030
Noturnal*Viviparous*Svl	0.110	0.020
Noturnal*Female*Svl	0.040	0.040
Residuals	0.400	

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Appendix 3 – Papers used to fill gaps on dataset

<i>Species</i>	<i>Mass reference</i>	<i>Svl reference</i>
<i>Acrochordus arafurae</i> (Mcdowell, 1979)	Seymour et al.,. (1981)	Presented by papers
<i>Agkistrodon piscivorous</i> (Lacépède, 1789)	Wharton (1966)	Presented by papers
<i>Bitis gabonica</i> (Duméril, Bibron & Duméril, 1854)	Database average	Database average
<i>Crotalus adamanteus</i> (Palisot De Beauvois, 1799)	Dorcas et al.,. (2004)	Database average
<i>Crotalus atrox</i>	Taylor and Denardo	Amarello et

<i>(Baird & Girard, 1853)</i>	(2005)	al.,. (2010)
<i>Crotalus horridus (Linnaeus, 1758)</i>	Gibbons (1972)	Gibbons (1972)
<i>Crotalus lepidus (Kennicott, 1861)</i>	Presented by papers	Holycross et al.,. (2002)
<i>Crotalus viridis (Rafinesque, 1818)</i>	Diller and Wallace (1984)	Diller and Wallace (1984)
<i>Eunectes notaeus (Cope, 1862)</i>	Presented by papers	Database average
<i>Enhydris enhydris (Schneider, 1799)</i>	Pongcharoen et al.,. (2008)	Presented by papers
<i>Hypsicopus plumbea (Boie, 1827)</i>	Karns et al.,. (2005)	Karns et al.,. (2005)
<i>Lampropeltis getula (Linnaeus, 1766)</i>	Jackson et al.,. (2004)	Presented by papers
<i>Lichanura trivirgata (Cope, 1861)</i>	Arnaud and Blazquez (2018)	Arnaud and Blazquez (2018)
<i>Morelia spilota (Lacépède, 1804)</i>	Pearson et al.,. (2002)	Pearson et al.,. (2002)
<i>Natrix natrix (Linnaeus, 1758)</i>	Gregory (2004)	Gregory (2004)
<i>Nerodia harteri (Trapido, 1941)</i>	Greene et al.,. (1999)	Shine (1991)
<i>Pantherophis obsoletus (Say, 1823)</i>	Penning (2018)	Penning (2018)
<i>Pituophis catenifer</i>	Iverson et al.,. (2008)	Pyron and

<i>(Blainville, 1835)</i>		Burbrink (2009)
<i>Pituophis melanoleucus (Daudin, 1803)</i>	Database average	Presented by papers
<i>Python bivittatus (Kuhl, 1820)</i>	Database average	Database average
<i>Rhabdophis tigrinus (Boie, 1826)</i>	Tanaka and Ota (2002)	Presented by papers
<i>Sistrurus catenatus (Rafinesque, 1818)</i>	Average of <i>S. miliaris</i> in dataset	Hobert et al., (2004)
<i>Sistrurus tergeminus (Say, 1823)</i>	Average of <i>S. miliaris</i> in dataset	Database average
<i>Bothrops asper (Garman, 1883)</i>	Medina-Barrios et al., (2019)	Presented by papers
<i>Chilabothrus subflavus (Stejneger, 1901)</i>	Database average	Presented by papers
<i>Heterodon platirhinos (Latreille, 1801)</i>	Database average	Cunnington et al., (2005)
<i>Pantherophis vulpinus (Baird & Girard, 1853)</i>	Average <i>P. obsoletus</i> in dataset	Pyron and Burbrink (2009)
<i>Pseudechis porphyriacus (Shaw, 1794)</i>	Shine (1987)	Presented by papers
<i>Vipera berus (Linnaeus, 1758)</i>	Andrén and Nilson (1981)	Andrén and Nilson (1981)

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**CAPITULO 2: THE SCIENCE BEHIND SNAKE
SLITHER: WHAT DO WE KNOW SO FAR
ABOUT SNAKES MOVEMENT ECOLOGY**

THE SCIENCE BEHIND SNAKE SLITHER: WHAT DO WE KNOW SO FAR ABOUT SNAKES MOVEMENT ECOLOGY

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ABSTRACT

Over the past few decades, numerous studies have been conducted on animal movement, including research into the movement patterns of snakes. However, despite the use of the same methodology, some studies have yielded divergent results when examining the influence of certain factors. Therefore, a review and analysis of these papers were required to identify the sources of variation that could account for the differences in their findings. We have searched for papers that utilized radio telemetry to track snakes, our searches were conducted systematically across the main online bibliographic platforms, resulting in a total of 319 relevant papers. These studies have primarily focused on a small number of well-studied snake species, with comparatively few papers available for other species. Through these studies, it has been observed that the movement patterns of snakes are largely driven by their need to maintain optimal metabolic conditions and avoid potentially dangerous situations. This includes regulating body temperature and hydration levels, maximizing opportunities for predation and reproduction, and seeking out secure shelter for rest. Snakes have the capacity to build a mental map of their environment, allowing them to navigate between the locations of the resources and shelter location with precision. Good shelters are reused and sometimes shared with other snakes or other reptile species. Snakes are also aware of the seasonal variations in the availability of resources, possibly by

recognizing signals of the seasonal changes and exhibiting behavioral responses to these changes. Conversely, as resources start to become scarce, particularly during the onset of the wet season or preceding winter, snakes reduce their movement rate. We expect that these results can guide future studies of snake movement to study the less studied trends and integrate their results in environmental contexts instead of draw isolated conclusions.

INTRODUCTION

Movement is a complex concept with multiple definitions and has been the target of several discussions about its definition over time. It was defined in the context of movement ecology as a change in the spatial position of an individual over time (Nathan et al., 2008, Holyoak, 2008). The movement has consequences, that is interactions between the individual with the external factors surrounding it, the nature of these interactions is influenced by the choices made by the individual during the movement process, like the choice of a good hunting spot can turn into predation success, the choice of a bad one can turn it into a prey of another animal (Nathan et al., 2008; Holyoak, 2008; Shaw, 2020).

Several studies of animal movement have been made in the last decades, the advance of telemetry and GPS technology brings new possibilities and allowed a big amount of data about different animal groups to be collected (Benitez-Paez et al., 2021). However, most of these papers focus on understanding specific movement patterns, normally studying the influence of one particular cause on individual movement and making no inference in the environmental context for other potential causes and the consequences (Holyoak, 2008; Shaw, 2020).

The study of snake movement is no exception. Several papers have been published around the world with different species finding different results. Previous studies found pieces of evidence of different factors in snake movement, coming from internal state like sex and age (Brown e Shine, 2002), pregnancy (Blouin-Demers, 2007) or body size (Hyslop, 2014). Other studies

indicate that movement can be influenced by external factors like temperature (Eskew e Todd, 2017), humidity (Daltry et al.,1998) landscape structure (Hoss, 2010), prey availability (Cristy, 2017), or intraspecific competition (Kjoss, 2001).

In some papers the influence of the same factors was investigated, yielding completely different results, as for the influence of sex, some studies affirm that males have larger movement rates than females (Petersen, 2019) other studies say that females have higher movement rates (Carrasco-Harris, 2020), other studies found no influence of sex on snake movement (Michael, 2014) and others affirm that this influence varies along the year (Smith, 2009). Considering that all the papers cited above used similar methodologies and found different results, the summarization and analyses of the results of these papers are fundamental to identifying and understanding the causes of these variations and finding clear conclusions. The present study aims to gather all knowledge available about snake movement, as well, identify the gaps of knowledge in snake movement ecology in order to use them more precisely in future studies.

METHODS

We systematically searched for papers that tracked snakes with radio telemetry in the Google Scholar, Core, Jstor, and BioOne platforms; in the online content of Journal of Herpetology, Acta Herpetologica, Copeia, Amphibia-Reptilia, and Herpetozoa, and all issues of the Herpetological Review and Salamandra - German Journal of Herpetology. We used the search terms: “snake” AND “movement” OR “home range” AND “telemetry”. We read all the papers and noted their main conclusions relative to snake movement and home range. We classified the trends of the studies according to a table adapted of Nathan et al (2009). We only included in our analysis papers that used radio telemetry to reduce the bias of the sample methodology and facilitate the comparison of the conclusions.

The species taxonomy was revised and updated according to the Reptile Database (<http://www.reptile-database.org/>) (Uetz et al, 2023) and the species

classified by family (according to Zaher et al., 2019, more details in Appendix 4). We noted the papers main conclusion relatively to snake movement and home range and classified the trends of the studies according with the following table adapted of Nathan et al. (2009). We also identified the study country (the country where the snakes were tracked, not the country of the first author) as well as the biogeographic region where the country is located.

The trends are classified following the diagram proposed by Nathan et al (2008) and adapted by Holyoak (2008) as showed in figure 4. **Internal state** is defined as the intrinsic motivation of movement, prevenient of factors inherent from the individual organism (eg. sex, age, size, hunger, preferences); **External factors** is defined as the external motivation of movement, from factors prominent form the physical and biological components of the environment surrounding the organism (eg. Temperature, terrain, pluviosity, prey availability, predator presence); **Navigation capacity** is defined as the organism's basic ability to move and affects where and when to move, any measure of individual orientation in a path, or consideration if the snake knows where its going. (eg. turning angles, direction analysis, fidelity); **Motion capacity** is the ability of the organism to move either under its own locomotion, any quantitative measure of how much an individual can move in a limited period of time (eg. distance daily moved, step size, speed);

Movement is the behaviour of move, changing the spatial position of the whole individual, and is divided in movement frequency or rate (quantity of events where the behaviour occur in determined period of time) and movement distances (the distance travelled during the movement event. In this case, it synonymizes with motion capacity). We used activity as a proxy of movement rate, because some studies used telemetry to quantify and monitor snakes' activity by following their movements thought time, the same methodology is used to quantify movement rate, in this context activity can be synonymized with movement frequency. The activity of a snake refers to the frequency at which it performs a particular movement behavior and is not synonymous with movement distance. Therefor, it can be accurately replaced with the term "movement frequency", but not with "movement distance"(Nathan et al., 2008;

Holyoak, 2008). **Space use** is a direct result of movement behavior and can be defined as the spatial extent occupied by the organism, including all the resources that it utilizes in its current spatial position. It encompasses how an animal utilizes the available space in its environment, taking into account its behavioral context (eg. home range, microhabitat selection or avoidance) (Krausman, 1999).

Survival refers to the ability of an individual to remain alive until the end of a monitoring period, and it is closely linked to movement and space use. In order to survive, an individual must locate and utilize the resources necessary to sustain its metabolic activities, while avoiding threats such as predators and other hazards. Therefore, movement and space use are critical for survival as they allow individuals to find and exploit the necessary resources, while minimizing the risk of predation and other threats (Moiron, 2020). **Intraspecies** and **interspecies interactions** are inevitable outcomes of an individual's movement, space utilization, and survival strategies. The movement patterns and spatial preferences of an individual impact their interactions with conspecifics and heterospecifics, including the selection of optimal hunting grounds, secure shelters, and competition for limited resources. These complex relationships between individuals and their environment have been the focus of numerous studies exploring the influence of movement and space utilization on these interactions (Ricklefs, 2014; Shaw, 2020). **Technical** are papers that proposed and tested methods for equipment appendix and not drew ecological conclusions.

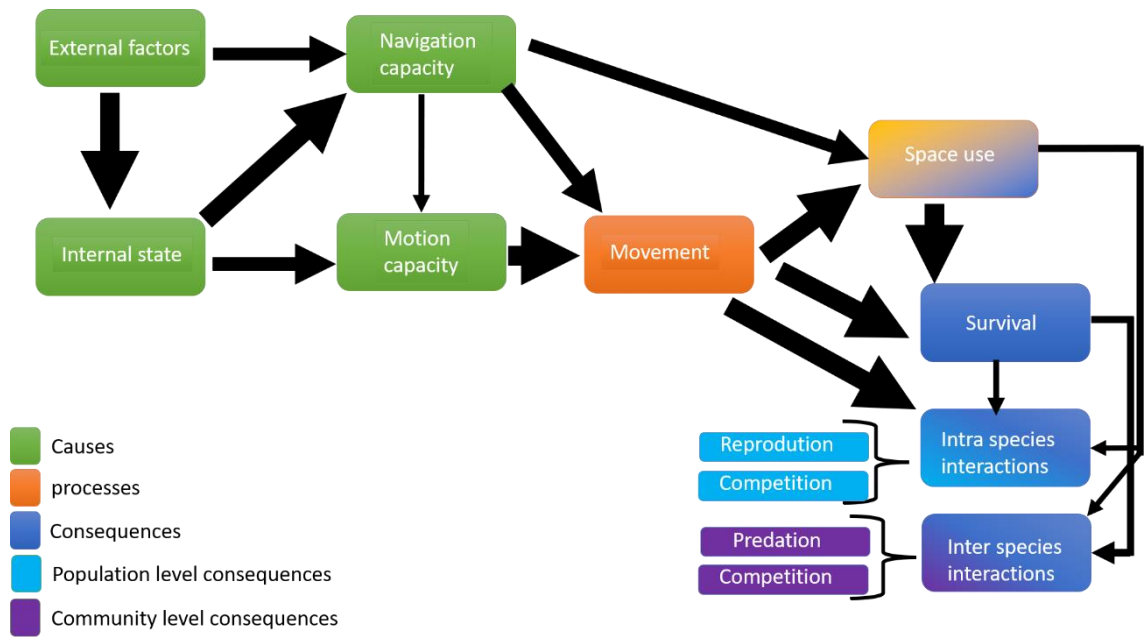


Figure 4: Movement ecology diagram adapted from Nathan et al 2008, Holyoak (2008) and Shaw (2020)

RESULTS AND DISCUSSION

We found a total of 319 papers and analysed 252 papers and build our database (exclusion criteria in fig.5). The studies used a total of 94 species divided in 10 families (23 papers worked with more than one species and four papers used species of different families). *Crotalus horridus* was the most studied species (26 Papers in total) followed by *Sistrurus catenatus* (20) and *Pantherophis obsoletus* (19). The majority of the species (47) were present in only one study. The most studied family was Viperidae (99 papers) followed by Colubridae (79) and Natricidae (29) (Fig.6).

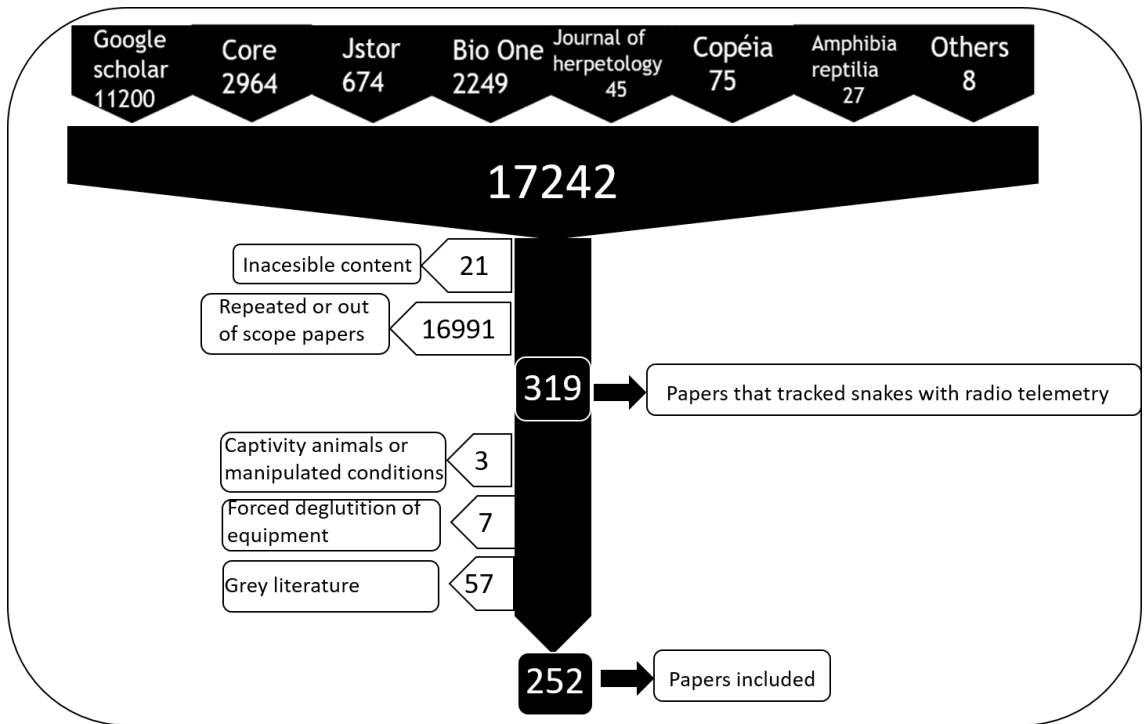


Figure 5: Criteria for selection of papers and exclusion filters.

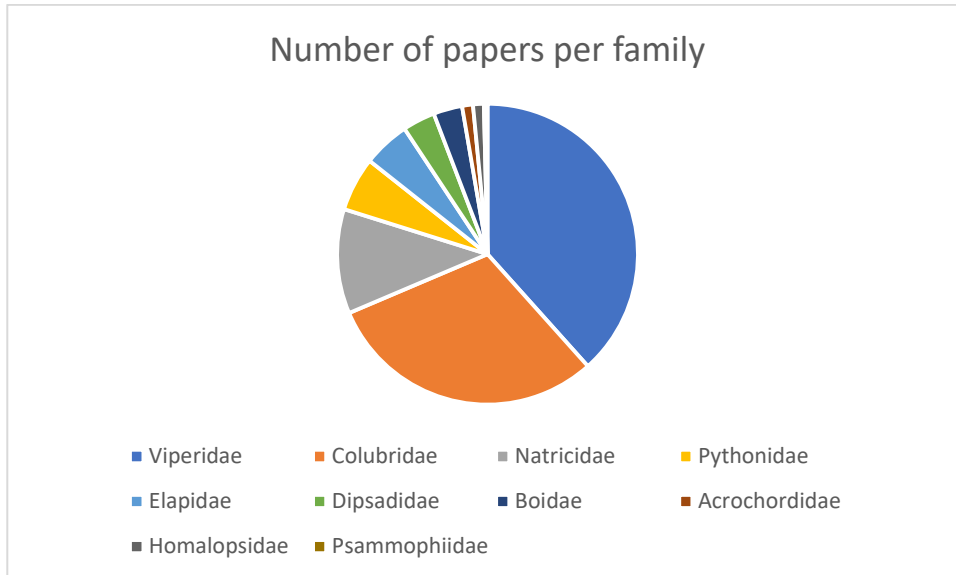


Figure 6 Number of studies per family using article search methodology on online platforms

Relative to the temporal distribution of papers (fig 7) 20% of them were published until 2000, 35 % were published from 2001 to 2010 and 47% from 2011 to 2020. Relative to spatial distribution of the papers, the largest majority of papers were

made in Nearctic biogeographic region (197 papers divided among 54 different species of six families) followed by Australian (28 papers divided among 15 species of four families) and Oriental (16 papers divided among 14 species of seven families) . The most studied country was USA (67% of papers on the territory and colonies), followed by Canada (11%) and Australia (9%).

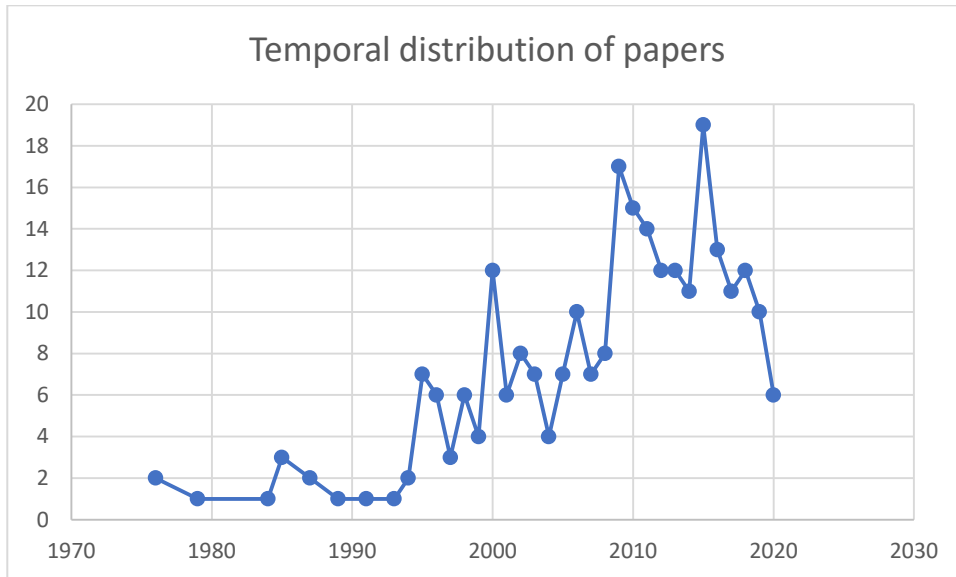


Figure 7 Temporal distribution of papers

The most studied trend was space use (33%) followed by external factors (32.5%), and movement (26.6%) (fig 8). The prevailing conclusion, independent of species, year or geographic region was that “males home range size is larger than females” (35, papers concluded this result), followed by “males exhibited higher movement rates than females” (24 papers concluded this result) and a tie between “males movement increase during mating season” (21 papers concluded this result) and “snakes utilized anthropogenic structures” (also 21 papers concluded this result).

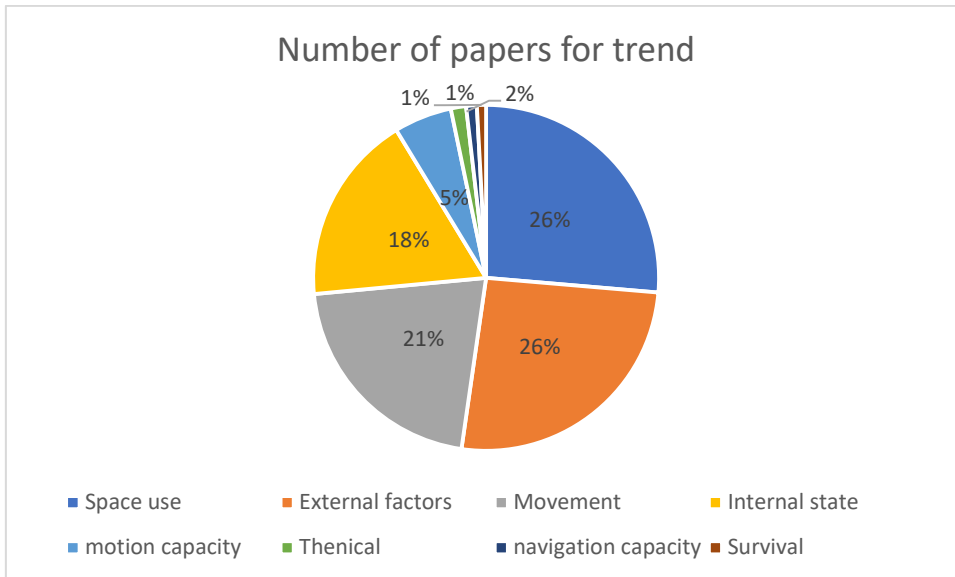


Figure 8 Number of papers for trend

Information concentration

Most data is concentrated in a few well studied species while other species have few papers (see more details in appendix 5. The great majority of the papers about movement and space use of snakes were made with *Crotalus horridus* in the USA. This tendency was constant since 1990 until 2019. Other usually studied species were *Sistrurus catenatus*, also from the Viperidae family and *Pantherophis obsoletus* from the Colubridae family. For these three species we have a large dataset available, for other 12 species we have between 5 and 10 papers and for the others 76 species we have less than 5, for 47 of them coi only one paper was available. This means that the most information in this field is concentrated in two species of one family living in the same geographic region.

In the Nearctic region of the 197 papers (Figure 9) , 87 (44%) are with 15 species of Viperidae family (27% of all studied species in the region), and 26 of them studied *C. horridus*. Also 166 (84%) of these papers were made in USA territory. In Australian region we have 11 (39%) for 28 papers with Pythonidae family, 10 (35%) with Elapidae family and three (10%) for Colubridae and Acrochordidae families. Seven papers (25%) are with *Morelia spilota*, the other species have from one to three papers. Also 34 (84%) of the papers were made in Australian territory. In the Australian region the data is more distributed among species and families, however still concentrated in

Australia country area. The concentration of studies with snake ecology in few species is reported from other areas (Plat, 2017; Rivas, 2005).

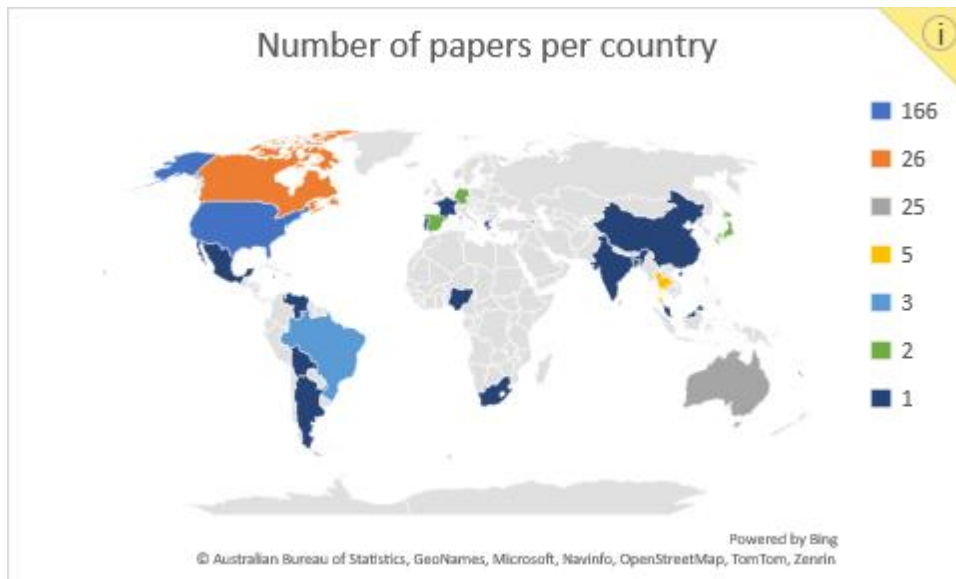


Figure 9 Number of papers per country

Trends discussed in papers

The majority of papers that utilized radio telemetry on snakes aimed to investigate the influence of external factors, which refers to the effects of environmental factors that are independent of the individual being studied (e.g., vegetation, surface and air temperature, and season of the year) on space use (52 papers) and movement (29 papers) (Nathan et al., 2009). The influence of internal factors, such as sex, age, SVL, and body mass, which vary between individuals and are independent of the environment, were the second most studied trend in space use (23 papers) and movement (21) papers, after the influence of external factors such as vegetation, surface and air temperature, and year season (Nathan et al, 2009). These findings are consistent with Holyoak's (2008) study, which identified external factors as the most frequently studied trend in movement ecology papers. However, Holyoak found that only 9% of the papers in their dataset considered the influence of internal factors, suggesting that snake movement ecology research is relatively more likely to examine the impact of internal factors compared to the broader field of animal movement ecology.

The trend Motion capacity [how much a snake can move in a determined period of time, therefore, the distance that an individual can travel in a certain time interval (Nathan, et al , 2008) is one of the less approached trends (37 papers). It differs from the movement trend because movement is a behaviour, dependent of a decision of the snake to start and to stop, while motion capacity is a measure of the limit of the utilization of the movement behaviour, it can be quantified (Nathan, et al, 2008). Not all papers that quantified snake movement addressed the motion capacity trend. We analyzed the trends discussed in the papers' conclusion and discussion sections. Few papers investigated the influence of internal state (seven) and external factors (five) on motion capacity. Others examined the impact of motion capacity on space use (eight) and movement (two). However, the majority of the papers did not consider this feature (Holyoak , 2008) (For more information see Appendix 3).

Ten papers dealt with the technical trend, which pertains to papers whose sole objective was to test a methodology, whether successful or not. Seven papers addressed the survival trend, where authors studied the effect of external factors (five papers), space use (one paper), and internal state (one paper) on snakes' survival rate using radio telemetry equipment. The least studied trend was reproduction, with only one paper investigating the impact of movement and space use on successful snake mating and offspring production. The trend of navigation capacity, which refers to the active selection of movement paths by snakes based on their orientation in space, time, and position, as well as the timing of movement events (Nathan et al., 2008), was examined in only seven papers. Of these, five investigated the influence of internal and external factors on navigation capacity and its effect on movement, one examined the influence of external factors on navigation capacity, and two explored the effects of navigation capacity on space use. Despite its significance, this trend was not extensively studied. Movement is the fundamental behavior that all other ecological processes in the diagram of Figure 4 are built around, including space use. Survival and reproduction are consequences of movement and space use. Although the majority of papers that used radio telemetry to study snake movement and space use focus on the behavior itself and its immediate consequences, few of them attempt to understand the underlying processes between the decision to move and the act of movement, the influence of movement on space use, and the ecological implications of movement and space use on the snake's life, such as prey capture success, competition, population abundance, dispersal, and survival (Nathan et al 2008; Holyoak, 2008).

Despite following the movement ecology paradigm proposed by Nathan (2008) to unify movement research across different groups, the majority of papers on snake movement and space use simply measure individual movement and investigate correlations with trends such as the influence of temperature on movement rate or differences in home range between males and females. However, few of these studies draw conclusions or inferences about the ecological implications of these correlations for individuals, populations, or the broader community. This tendency is not unique to snake movement and space use research, but has been reported in other literature reviews such as Baguette (2004) and Holyoak (2008), suggesting a broader issue within the field of movement ecology.

Main conclusions

Reproduction and sex

From 45 studies that tested the influence of sex on movement, 34 (75.5%) of them concluded that male snakes have larger home ranges than females (see more in appendix 1). Studies also report that males increase their home range during the mating season to search for females (Slip and Shine, 1998; Smith, 2009). And during this period males also increase their movement rate (see more in appendix 1). Males also show higher movement rates than females (see more in appendix 1), however Smaniotto (2020) and Sperry (2012) report females moving more than males, and Carrasco-Harris (2020) found that the females movement more except during the breeding season, corroborating with Timmerman (1995) who observed female movement decreased during the breeding season. Also, authors reported that gravid females move less than nongravid (see more in appendix 1).

This can be explained by the mating behaviour of some snakes being polyandric, where females remain still in a safe location and several males attempt to copulate with a single female. This way females copulate with several males, leading to multiple paternity clutches. However in some species males remain with the same female until the end of season (Rivas, 2005). As some males will invest all their resources in a single female, they will search carefully to choose the most fertile female they can find. They rarely feed and their mortality rate increases (Bonnet, 1999; Whithaker and Shine, 2000, Rivas, 2005; Sperry, 2009; Olson, 2015). Despite of the necessity for search for females Smith (2015A) concluded that home range size does not influence males mating success. However, Leuemberger (2019) concluded that female home range sizes were larger than males. Also, some papers detected no

influence of sex on home range size (Bauder, 2015; Buchanan, 2018; Ettlign, 2013; Howze, 2015; Murray, 2010; Quintana, 2017; Shine, 1987; Wunderle, 2004; Zappartoli, 2015). A similar pattern was observed by Kerr (2006) in male lizards, where long movements in absence of food lead males to reach females early and also show their vigor to them.

Several authors report an increase in male movement rate and distances during the mating season (see more in appendix 1), only Sperry (2009) reports an increase only in females movement. Beale (2016) found increased movement for both sexes. Roth (2011) also presents evidence that the movement path of males during the mating season presents an active avoidance of other males and an attraction by females. Suggesting that females search and keep secure locations to oviposition while males search for reproductive females during the mating season, a variable home range being a result of maximizing their chance to encounter females (Wilson,2006).

Authors report home range overlaps among individuals of the same specie (Diffendorffer, 2005; Plumer, 2020; Slip and Shine, 1998; Vanek and Wasko, 2017; Wilson,2006). Steen (2009) affirms that these overlaps are more common between sexes, even so some authors reports overlaps among individuals of the same sex (Murray, 2010; Timmerman, 1995; Bauder, 2019; Strine, 2018).

Different from males, females do not change their home range size during the mating season (Wilson, 2006). However their home range size decreases during pregnancy becoming smaller (Gardner-Santana, 2009; Johnson, 2000; MacGowan and Walker, 2013; Parker e Anderson, 2007; Petersen, 2019; Roth, 2005; Webb and Shine, 1997). Only Schuett (2013) reports that reproductive status does not influence home range size independent of sex. Kerr (2006) found similar behaviour in lizards, reporting lower movement and activity rates for females, however after mating they increase their activity rate for a while, suggesting that during the mating season, females avoid movement to save energy for the gestation and oviposition period.

Wilson (2006) also reports that females have a stable home range size that overlaps with that of other females, while juveniles and adult males have significant variations in their home range size and area. The author also reports that several males cross the home range of a single female. Further females found and stay close to the hibernacula that will be used to oviposition while males travel far away of theirs and may found another to rest after mating (Reinert, 1988; Anderson, 2010). There are differences in habitat preference patterns between males and females (Angelici, 2000;

Hand, 2019; Wunderle, 2004). Reinert (1998) present differences in habitat preferences in females during pregnancy and Williams (2015) and Withing (1997) found changes from pregnancy to oviposition period, in general females use less microhabitats than males (Angeli, 2000) and spend less time exposed (Wunderle, 2004).

Body size

Movement patterns can be influenced by specific individual differences, such as shedding period, where snakes tend to be more sedentary (Mertens, 1994), and age, where young snakes tend to move more frequently however covering short distances while adults tend to be sedentary, but move large distances from time to time (Pizzatto, 2009). However Wilson (2006) found no influence of age on movement. Snout-vent length (SVL) is also a factor that can influence snake movements, where larger individuals tend to move larger distances (Bertram, 2001; Tozetti, 2009; Wilson, 2006), despite some studies finding no evidence of SVL on movement (Sperry, 2010; Michael, 2014). SVL can also influence positively the snake's home range (Dodd and Barichivich, 2007; Hyslop, 2014; Roth, 2005; Shine, 1987; Wilson, 2006), with large snakes presenting large home range, despite some authors finding no relation of SVL and home range size (Buchanan, 2017; Murray, 2010; Quintana, 2017; Secor, 1994). In addition, there are evidences of the influence of SVL in micro habitat selection, where larger individuals tend to be more exposed while lesser ones tend to be in shelters (Shine and Shine, 2003; Michael, 2014). Both age and SVL differences can be explained by snake audacity, and apparently small snakes tend to be more shy and make shorter movements being more careful, in fact there are evidences relating snake mortality to distance traveled (Bonet, 1999; Hyslop, 2009). Some studies also detected variations of unclear sources among individuals and attributed them to random effects (Diffendorffer, 2005; Gomez, 2015; Marinez-Freiria, 2018).

Home range size is not influenced by individual body mass (Murray, 2010; Quintana, 2017; Secor, 1994), none of the studies in our database found contrary evidences. This can be due to the fact that body mass in snakes show large variations. There are reports of variation among years (Shine et al 2000B), individual health condition (Gimmel, 2021), seasons and sexes (Gregory, 2011). Also, both sexes experience fasting periods where they consume their fat reservoir. In males this period is during the mating season, their highest peak of movement rate, as discussed above

(Rivas, 2005; Gregory, 2011), and in females during pregnancy, their lowest peak in movement rate as discussed above (Lourdais, 2002; Gignac, 2005). All this source of variation makes it difficult to find a significative correlation with body mass.

Seasonality

Seasonality is among the most commonly cited factors that influence snake movement, as noted in various studies (Gannon and Secoy, 1985; Marques et al., 2001; Eskew and Todd, 2017; Teffo, 2023). The effects of seasonality on snake movement patterns may be more pronounced in temperate snake communities, where the seasonal variations are more distinct, as opposed to tropical snake communities, where such variations may be less noticeable (Eskew and Todd, 2017).

Several authors found differences in home range size and movement patterns among biogeographic realms. In the Nearctic region snakes move less frequently and shorter distances during cooler seasons, especially during winter, snake's home range also shrink and become more stable. However, during hotter seasons, specially during spring, the movement rate and distances as well as the home range size increase (Timmerman, 1995; Diffendorffer, 2005; Blouin-Demers , 2007; Wastel, 2011; Miller, 2012; Pierce, 2014;). While males increase their activity and basking during spring and reduce their rate during summer, females maintain a stable rate of both behaviors during spring, summer and fall, only decreasing during winter (Sperry, 2009). Despite the movement directions being random throughout the year, during fall snakes tend to direction their movements to shelters where they will spend the winter (Secor, 1994). During winter there is a decrease in surface activity, while snakes remain in shelters most of the time (Timmerman, 1995; Wastel, 2011). Snakes make substantial movements frequently during early winter (Pierce, 2014) and few movements during late winter, mainly underground (Nordberg, 2017). There are registers even of change from diurnal to nocturnal activity during summer (Sperry, 2010).

In the Palearctic Region, as well in the Nearctic, snakes tend to increase their movement rates and home range sizes during spring (Marinez-Freiria, 2018), remain hidden in shelters during winter (Mertens, 1994; Marinez-Freiria, 2018) and have individual random movement in fall and summer(Marinez-Freiria, 2018). However, Brito (2003) describes two annual peaks of activity a minor one in spring and a major one in early-mid fall. The daily activity pattern of vipers in spring and autumn was unimodal,

whereas in summer they expanded their activity from early morning to late afternoon, and were also active at night. Mating season is apparently restricted to fall, and spring mating is either absent or very reduced (Brito, 2003).

In the Australian region, there is an increase in movement rate during the wet season, the early wet season (spring) is the mating season, where males movement and home range increase and the home range overlap increase in both sexes (Slip and Shine, 1988), while during the late wet season (summer) the home range overlap among home range of adult individuals of either sex decrease, suggesting that they avoid conspecific individuals during this period, maybe to avoid intraspecific competition and storage resources for the dry season (Webb, 1997). During the dry seasons (winter and fall) snakes tend to be more sedentary and spend more time in shelters (Shine and Lambeck, 1986; Slip and Shine, 1988; Webb, 1997; Whitaker and Shine, 2002; Wilson, 2006; Christian, 2007; Corey, 2010). Snakes also utilize areas propense to flood during the the dry season and all individuals leave these areas at the start of the wet season (Madsen, 1996).

Although data is limited, snake movement patterns in the Neotropical region are thought to follow a pattern similar to that observed in Australia. Specifically, snakes tend to have larger home ranges during the wet season, and exhibit greater shelter fidelity and sedentary behavior during the dry season (Tozetti, 2009; Quintana, 2017). During the wet season, male snakes increase their movement rate in order to search for mates, while some species - such as *Crotalus durissus* - maintain consistent activity rates throughout the year (Tozetti, 2013).

In the oriental region, we have the second major gap of data, only behind the Ethiopian region with no data about seasons influence on snake movement. Males' movement peak is during spring, summer and early autumn. Both sexes become sedentary during late autumn until the end of winter (Jung-Yung, 2009).

In all temperate mesoregions one pattern clearly influences snake movement the same way in all of them, snakes tend to be more active in warmer months (summer and spring) and inactive in colder months (winter and autumn). In Tropical mesoregions, despite the lack of data we can observe that the activity peak is in the wet season while in the dry season snakes tend to be more sedentary. Also, the mating season is in the time of the year where resources are more abundant (spring or wet season). Corroborating with the results of Eskew and Todd (2017) that says that the seasonal variation in snake movement is due to environmental factors that fluctuate

seasonally, in the temperate snake assembles the main factor seems to be temperature, however in tropical snake assembles where temperature does not present strong fluctuations the main factor seems to be humidity. We will discuss specifically about the influence of temperature, humidity and pluviosity in snake movement now:

Temperature

The effect of temperature on ectothermic animals' movement capacity is well debated in literature (e.g. Huey, 1982; Peterson et al., 1993; Eskew and Todd, 2017; Signore, 2022; Díaz-Ricaurte and Serrano, 2020; Díaz-Ricaurte et al., 2020; Diaz-Ricaurte et al., 2022). A decrease in body temperature leads to substantial reductions in sprint speed in lizards, swimming speed in fish, and jumping distance in frogs (Huey and Bennett, 1987; Hirano, 1984 Rome, 1990). Snakes are not different, snake movement is dependent of temperature in different levels like crawling speed, swimming speed, tongue-flicking rate, digestive rate, oxygen consumption (Stevenson, 1985) movement rate and distance moved (Eskew and Todd, 2017; Signore, 2022).

In our database, several authors found a positive relation between air temperature and movement frequency (Mertens, 1994; Nelson, 2000; Neuman, 2011; Weatherhead 2012), movement distance (Rao, 2013) and even the decision of when to move (Whitaker e Shine, 1999). However, this relation is not necessarily linked to air or substrate temperature, since Mertens (1994) reports activity even when air temperature is low, but intense sunlight is available. In these cases snakes spend more time in thermoregulation and Rao (2013) affirms that snakes tend to thermoregulate to maintain their body temperature in an optimal range, and the time spend in thermoregulation is dependent of the environment temperature.

Thermal quality is reported as the main predictor of snake's habitat selection in the Palearctic (Lelièvre, 2010; Kovar, 2016), Australian (Fitzgerald, 2003) and Nearctic regions (Blouin-Demers, 2002; Row, 2006; Goulet, 2015; Fortney, 2012). Snakes tend to select habitats in way to optimize their thermoregulation, this way they can maintain their body temperature above the temperature of the shaded environment, seeking for microhabitats with more solar incidence (Goulet, 2015; Fitzgerald, 2003; Díaz-Ricaurte and Serrano, 2021; Diaz-Ricaurte et al., 2022) or more thermoconservative (Mertens, 1994; Goulet, 2015; kovar, 2016), however they thermoregulate more effectively in spring (mating season) than in autumn or summer (Row, 2006). Also some species are

more thermophilic than others and utilize habitats with higher thermal quality more frequently (Lelièvre, 2010).

Some authors found that thermal quality is not the main driver of snake's habitat selection. Daltry (1998) found snakes being more thermoconformers, and affirms that humidity is the main driver of habitat selection and activity in the oriental region. Sperry (2010) affirms that snakes can be capable of adapting to disavowable temperatures and their activity is more linked to reproductive season, at least in the north of the Nearctic region.

Humidity

For the oriental region, Daltry (1998) and Rao (2013) affirm that relative humidity is the main factor influencing snake movement, also in low humidity environments underground activity increased. The authors also reported an increase in body exposition with humidity and the absence of basking thermoregulatory behavior, these snake species are completely thermoconformers and their behavior is focused more in preventing dehydration than in gaining heat. In the Nearctic region, despite is not being the main driver, activity and body exposition increases with air humidity, also despite the importance of temperature in temperate regions snakes tend to avoid excessive temperatures to avoid dehydration (Brito, 2003; Howze, 2012A; Moore, 2006).

As discussed by several studies, the drivers of snake movement are influenced by environmental factors, and the patterns of movement vary between tropical and temperate regions (Eskew and Todd, 2017; Tozetti, 2009). Snakes move to maintain their body temperature in an optimal range that maximizes metabolic efficiency and hydration levels (Maritz et al., 2016; Petersen et al., 2019). In temperate regions where temperatures are lower, keeping warm is more important than staying hydrated, while in tropical regions where temperatures are higher, keeping hydrated is more important (Eskew and Todd, 2017). These tendencies are reflected in the mating season and peaks of snake activity, which occur during the warm season in temperate regions and during the rainy season in tropical regions (Tozetti, 2009).

Pluviosity

It is essential to distinguish between air humidity and rain as environmental factors affecting snake movement. Although rain can increase air humidity levels, these factors can affect snake movement in distinct ways (Quintana, 2017; Shine and Lambert, 1986). Additionally, it is worth noting that the increase in movement and home range during the wet season in tropical regions, as discussed earlier, may not be directly linked to rainfall events (Christian, 2007; Quintana, 2017; Wilson, 2006). None of the authors affirmed that this increase in movement and home range is solely due to rain events. In the Palearctic region, Mertens (1994) affirms that movement rate decreases with rainfall because of the reduction of temperature caused by body contact with water. In the oriental (Daltry, 1998) and Australian (Buttler, 2005) regions, authors found no correlation between movement and rainfall. Differing from temperate regions, the rain seems not to affect the snake movement, probably because even during a rain the environment temperature decrease is not so accentuated as in temperate regions allowing snakes to maintain their activity. Portillo (2022) found that optimal pluviosity range is a main driver of snake's distribution in tropical forests and its influence decrease with latitude.

Some studies found an increase in home range area in the months with higher pluviosity in snakes that use flooded habitats, this relation is due to the increase of flooded area used as habitat by these species (Goulet, 2015; Quintana, 2017; Plumer, 2020), however non-aquatic species avoid flood areas and have a decrease in home range during flood period (Madsen, 1996; Halstead, 200). Thus, we can affirm that the influence of flooding on snake movement is dependent of habitat selection patterns of each species.

Intra and inter species interaction

Martino (2012) reports that the movement distance and home range of the same species increases with latitude. Several authors found differences in movement and home range patterns of two close populations of the same species (Withing, 1996; Jellen, 2007; Mead, 2018) what can be due to differences in habitats available in these close regions and corroborates with Kjoss (2001) who affirms that home range size is restricted by intraspecific competition. Evidences of the influence of inter specific competition area also available, Kjoss (2001) reports that the presence of *Coluber constrictor* in the environment reduce the abundance of large bodied snakes of other species, also despite filogenetically close species have similar movement patterns (Beck, 1995; Klug, 2011), several authors found differences in movement and home

range patterns between close related species living in the same environment (Beck, 1995; Roe, 2003; Lelièvre, 2010; Mitrovich, 2018; Leuenberger, 2019) these differences can be due to competition avoidance.

As discussed above, the presence of sexual partners (Wilson, 2006) and sexual competitors (Steen, 2009) influence snake movement and space use. However, the presence of individuals of different species also can influence snake movement patterns. Snake movement directions and home range location tend to point to locals where prey abundance is high, also the frequency of movement tend to follow the abundance peaks of prey (Weatherhead, 1985; Slip and Shine, 1998; Blouin-Demers, 2001; Crysti, 2017). Crysti, (2017) found an almost immediate response in movement patterns of *Boiga irregularis* to suppression in their prey population. The snakes increased their movement rate and their home range to search for a new area to hunt. Other studies show an increase in movement rate in less suitable and productive habitats (Beaupre, 1995; Gerald, 2006). Also, Kjoss (2001) reported a major abundance of snakes in habitats with higher species richness.

Snakes tend to be sit-and-wait predators or active searchers, some snakes alternate between these strategies and there are differences in microhabitat selection among hunting strategies of species (Bertram, 2001). Also habitat selection influences individual predation success rate and diet (Blouin-Demers, 2003). The location of snake home ranges affects other nearby species abundance. Klug (2010) found that the presence of snakes in forest fragments reduce the nest survival, mating success and abundance of birds in comparison with close fragments where snakes are not present.

Shelter

Most snakes tend to be sedentary animals, avoiding move, unless its really necessary (Shine e Fitzgerald, 1995; Voris, 1996; Blázquez, 1995; Karns, 2000; 2002; Kingsbury, 2000; Ealy, 2004; Bell, 2007; Harvey, 2014). So, the shelter is crucial to snakes' survival, both in temperate regions to hibernate, and in tropical regions to hide after feeding to digest, to lay eggs or wait to give birth (Mullin, S. J., and Seigel, 2009). The shelter also influences snake movement and space use behaviour, movement direction generally pointed to shelters (Secor, 1994), home range and core areas are generally centred around one or more shelters (Ealy, 2004; Harvey, 2006; Gardiner,

2015; Hand, 2019). There are registers of shelter shared with other snakes from the same and from different species, also with other reptiles and amphibians (Wastell and Mcenssy, 2016)

Several studies found snakes using the same shelter in different years (see more details in appendix 1). Yagi (2020) found this behavior even after human alteration of the environment. Some authors found snakes using the same home range area, with few variations in its size through the years (Tozetti, 2009; Wilson, 2006; Smith, 2009). This is more common in adults than in neonates (Waldron, 2013; Webb, 1997; Wilson, 2006) and in females than males (Wilson 2006). Not all snakes of the population present this behavior (Williams, 2012;2015) and in some studies it was not observed (Pierce, 2014; Sperry, 2009)

The occurrence of these behaviors and the results of Baxley (2009), Bell (2007), Bertram (2001) and others (see more in appendix 1) affirm that home range locations tend to be where more resources are available, being an indicator that snakes know where the resources necessary for their survival are located. The higher frequency of home range fidelity in adults than neonates (Waldron, 2013; Webb, 1997; Wilson, 2006) can be an indicator that the knowledge comes from experience.

Other evidences that support this affirmation are the differences in movement and space use behaviours between resident snakes (individuals that were born and grew in that locations) and translocated snakes (individuals that were born and grew in a different location and for some reason where introduced into a new area). First of all, a translocated snake tends to return to its original place when this is possible (Brown, 2009; Galigan, 1979; Nowak, 2002). They also have site fidelity lower than resident snakes, and this difference is reduced when the translocated pass through a acclimation process (Sacerdote-Velat, 2014). Translocated snakes also have higher movement rates than resident (Butler, 2005; Nash and Griffiths, 2018; Reinert, 1999; Roe, 2010; Wolfe, 2018; Brown, 2009), and lower movement frequency (Roe, 2010), what means they perform few movement events, however with large distances. Only Butler (2005) found no difference between the movement pattern of translocated snakes.

Translocated snakes also have differences in home range size, in some cases they have higher home range sizes (Wolfe, 2018) in others they can have no significant difference in home range size between translocated and resident

individuals (Nash and Griffiths, 2018). Reinert (1999) found differences in habitat selection between translocated and resident snakes.

The knowledge of the surrounding environment affects individual survival, translocated snakes have higher mortality rates than resident (Nowak, 2002; Reinert, 1999; Roe, 2010; Wolfe, 2018), however translocated snakes that have received acclimatation have lower mortality rates than those who have not (Sacerdote-Velat, 2014). Also, De Gregorio (2017) found differences in movement and space use of the same individual after a period in captivity.

Circadian cycle and light

Movement is also affected by illumination conditions, being nocturnal species increasing their movement at night (Shine and Lambert, 1985; Voris, 1996; Tozetti, 2009), diurnal species presenting a positive relation between movement rate and sunny days (Butler, 2005; Mertens, 1994) and light intensity during day (Howze, 2012), and some snakes can alternate between day periods (Karn, 2000). Snakes' microhabitat selection is influenced by the circadian cycle as well, during inactive period snakes tend to seek for shelter and during active they normally seek for prey and utilize hunting spots (Wasko, 2010). Eskew and Todd (2017) affirm that moonlight increases the activity of nocturnal species and decreases that of diurnal species. Snakes' visual adaptations are very diverse, nocturnal species have large and more sensitive eyes that can receive the low light available and diurnal snakes have protective adaptations to cut UV radiation and protect the corneas, therefore the influence of circadian cycle is linked to the presence of these adaptations (Simões, 2016).

Vegetation structure

The vegetation structure has influence in home range location, there are evidences showing the influence of shrubs abundance (Gardiner, 2015; Halstead, 2009; Mata-Silva, 2018), positive relation with canopy cover (Zappatoli, 2011), negative relation with canopy cover (Goulet, 2015; Waldron, 2008, Weatherhead, 1985) and soft-mast presence (Heres, 2018). Michael (2014) found an increase in home range area where the vegetation structure can support a low diversity of consumable prey for snakes. As discussed above, snakes tend to move in direction of the resources they seek, however it's not clear if this relation reflects the ability to

locate the resources or the knowledge to recognize the vegetation features where these resources are more easily found. The study of snakes navigation capacity is scarce however we presented evidences that snake movement is non-random (larsen, 1987; Clark,2005; Linn, 2006 Pizzatto, 2009; Kojima,2014; de Gregorio, 2015; Hart, 2015; Gomez, 2015;Goetz,2016) and have evidences that snakes have a navigational map of their habitat and compass senses (Pittman, 2014).

Soil characteristics

There are studies showing that the influence of soil features on snake movement and space use are influenced by soil characteristics. There is a positive influence of the presence of ground debris and rock cover on home range location, these structures are thermoconservatives and can be used as shelter (Goulet, 2015). There are reports of snakes that present digging behaviour haveing preference for sandy loam soils (mainly composed by sand, but with enough clay to be fertile) where are easier to dig (Lagory, 2009). Digging snakes living in flood plains have preference for deep soil with high permeability wich allows to drain more water and is less propense to flood (Wagner, 2014).

Environment and antropogenic disturbance

Some studies investigated the influence of natural disturbances on snake movement. No influence of fire history on movement was (Cross, 2015; Flaherty, 2020), however Howey (2016) found a preference for burned grounds to thermoregulate. Wunderle (2004) found an increase in movement rate after a hurricane in arboreal species. The author affirms that this is due the fact that the hurricane damages the vegetation used by Boas as habitat and they have to seek for new trees to use as shelter or hunting spot. Similar results were found by Rao (2013) who registered a positive relation between movement rate and wind speed probably because of the same reason.

The presence of anthropogenic structures in the environment and human management of the environment decrease the snake's survival (Bailey, 2011; Breininger, 2012), health condition (Wylie, 2010), and movement rate (Corey, 2010). Several studies found a tendency in snakes to avoid anthropogenic structures (Akresh, 2016; Angelici, 2000; Bauder, 2015; Baxley, 2011, Moore, 2006; Robson, 2013; Rudolph, 1997; Shepherd, 2008; Wasko, 2010).

Some species seem to tolerate human management having no alteration in their home range size (Corey, 2010; MacGowan and Walker, 2013), others can increase their home range in human altered habitats (Weatherhead, 2010; Ettlign, 2013; Lomas, 2019). This behaviour is more frequent in males (Ettlign, 2013). Several papers registered snakes utilizing anthropogenic structures for thermoregulation and shelter (see more details in appendix 1) and some studies registered preference for these structures (Titus, 2007; Radke and Walkom, 2008; Raman, 2014). This tendency is stronger in females (Radke and Walkom, 2008) .

Final considerations

Here we present a compilation, analysis and summarization of published knowledge on snake movement. All the papers included in our analysis utilized radio telemetry to monitor activity, movement, survival and other features of snake behavior, thus the conclusions compared to the present study were made using the same methodology, reducing the probability that the differences between papers were prevented of sample bias. The papers investigating snake movement follow the tendency described by Holyoak (2008) investigating the influence of some environmental factors on movement or home range, without discussing the relation of causes and consequences in the populational, community and ecosystem context. Also the majority of papers do not present their movement data on the paper.

The movement patterns of snakes are determined by their need to maintain optimal conditions for metabolic activities and avoid potentially lethal conditions. This includes regulating their body temperature and hydration levels, which are essential for maximizing predation and reproduction success, as well as finding a secure shelter for rest. In fact, the availability of suitable shelters is the most important factor influencing their home range. According to Shine and Lambert (1986) and Wilson (2006), snakes have a mental map of their environment and are capable of locating resources and returning to their shelters. They frequently reuse good shelters and may even share them with other snakes or reptile species. Additionally, snakes are attuned to seasonal variations in resource availability and may increase their movement rate to find mating partners during abundance seasons (such as spring and wet season), while reducing their movement rate when resources begin to become scarce (start of wet season or approaching winter) (Cristian, 2007; Quintana, 2017).

We expect that these results can help future studies with snake movement to link their conclusions with the environmental and ecological context instead of draw

isolated conclusions. We also expect to encourage scientists to explore the less explored trends like navigation capacity and survival, investigate the impact of individual movement in population, community and ecosystem context and what causes and consequences this behavior have.

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Appendix 1: Complete citations

Males have larger movement rates than females

(Anderson, 2010; Angelici, 2000; Bauder, 2019; Brown and Weatherhead, 1999; De Gregorio, 2011; Durbian, 2008; Ettling, 2013; Godwin, 2011; Hand, 2019; Hyslop, 2014; Jung-Yun, 2009; Kapfer, 2008; Lee Et Al, 2009; Linehan, 2010; Macgowan and Walker, 2013; Mead And Stark, 2018; Miler, 2012; Nilson, 1999; Parker E Anderson, 2007; Patten, 2016; Petersen, 2019; Reinert, 1998; Richardon, 2006; Roth, 2005; Roth, 2011; Sealy, 2002; Shine, 1996; Slip and Shine, 1998; Timmerman, 1995; Wastel, 2011; Withing, 1997; Wunderle, 2004)

Males have larger home range than females:

(Blouin-Demers, 2007; Brown, 1977; Carrasco-Harris, 2020; Daltry, 1998; De Gregorio, 2011; Dubey, 2008; Hand, 2019; Howze, 2015; Jung-Yung, 2009; Kapfer, 2008; Linn, 2006; Miesma, 2011; Mohr, 2012; Moriarty, 1991; Parker E Anderson, 2007; Petersen,

2019; Sealy, 2002; Secor, 1994; Slip and Shine, 1998; Sperry, 2010 ; Titus,2007 ; Wilson, 2006; Withing, 1997; Nash and Griffiths, 2018)

Habitat selection is influenced by resources available:

(Blouin-Demers, 2001; Ealy, 2004; Gardiner, 2015; Goulet, 2015; Halstead, 2009; Hand, 2019; Harvey, 2006; Heres, 2018; Kovar, 2016; Larsen, 1987; Mata-Silva, 2018; Michael, 2013; Quintana, 2017; Shine E Shine, 2003; Waldron, 2008; Weatherhead, 1985; Zappartoli,2011)

Home range location is influenced by resources available:

(Baxley, 2009; Bell, 2007; Bertram, 2001; Brown, 1976; Ealy, 2004; Jellen, 2007; Kingsbury, 2000; Leuemberger, 2019; Madsen, 1996; Martino, 2011; Mata-Silva, 2015; Nilson, 1999; Waldron, 2008)

gravid females move less than nongravid

(Buchanan, 2017; Carrasco-Harris, 2020; Charland, 1995; de Gregorio, 2011; Gardner-santana, 2009; Johnson,2000; Kojima, 2014, mohr, 2012; Parker e Anderson, 2007; Webb, 1997; withing, 1997)

Males movement increase during the mating season

(Anderson, 2015; Bauder, 2019; Carrasco-Harris, 2020; Coupe, 2002; De Gregorio, 2011; Hand, 2019, Howze, 2015; Hyslop, 2012; Jung-Yung, 2009; Petersen, 2019; Rouse, 2011; Secor, 1994; Shine, 1987; Shine, 2000; Slip and Shine, 1998; Smith, 2009; Sperry, 2009; Timmerman, 1995; and Tozetti ,2009 ; Tozetti, 2013; Wilson, 2006; Wunderle, 2004)

Snakes using the same shelter in different years

(Anderson, 2010; Bertram, 2003; Bell, 2008; Brown, 1977; Jellen, 2007; Kapfer, 2008; kingsbury, 2000; Reinert, 1998; Shine,1987; Smith, 2009; Yagi, 2020).

Snakes utilize anthropogenic structures for thermoregulation and shelter

(Baxley, 2009; Bertram, 2002; Blouin-Demers, 2003; Burger and Zappartoli, 1998; Carter, 2012; Corey, 2010; Crane, 2016; Ettling, 2013, Fortney, 2020; himes, 2001; kovar, 2016; Marshal, 2019; Miler, 2012; Radke and walkom, 2008; rhaman, 2014; Shine, 1996; Sperry, 2008; Titus, 2007; Wilson, 2018; Yagi, 2020; Halstead, 2019

Appendix 2: Papers included on analysis

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Appendix 3: Papers and trends aborded.

Auhtor	Year	Trends
Buttler	2005	Movement, External Factors
Corey	2010	Space Use, Movement, External Factors
Cristian	2007	Movement, External Factors

David and Shine	1998	Space Use, Movement, Internal State
Dubey	2008	Motion Capacity, Internal State
Fitzgerald	2003	Space Use, External Factors, Internal State
Madsen	1996	Space Use, Movement, External Factors
Pearson	2003	Space Use, External Factors, Internal State
Pizzatto	2009	Movement, External Factors, Internal State
Pratt	2010	Movement, External Factors Movement, Motion Capacity, Internal State, External
Shetty E Shine	2002	Factors
Shine	1985	Movement, Space Use, External Factors
Shine	1987	Movement, Space Use, External Factors, Internal State
Shine	2009	Movement, Space Use, Internal State, External Factors Space Use, Motion Capacity, Internal State, External
Shine	1996	Factors
Shine E Fitzgerald	1995	Movement, Internal State
Shine E Lambert	1985	Motion Capacity, Space Use, External Factors
Shine E Shine	2003	Space Use, Internal State, External Factors
Siers	2014	Movement, Space Use, External Factors
Siers	2018	Movement, Internal State
Slip and Shine	1998	Movement, Space Use, External Factors, Internal State Space Use, Movement, Internal State, External Fac-
Webb	1997	tors, Motion Capacity
Wilson	2006	Space Use, Movement, Internal State, External Factors
Whitaker E Shine	1999	Movement, Internal State, External Factors
Whitaker E Shine	2000	Movement, External Factors
Whitaker E Shine	2002	Movement, Space Use, External Factors
Wolfe	2018	Space Use, Movement, External Factors
Angeli	2000	Space Use, Internal State, External Factors,
Linn	2006	Space Use, Internal State
Adams	2005	Space Use, Internal State, Motion Capacity
Akresh	2017	Space Use, External Factors
Anderson	2010	Movement, Navigation Capacity, Internal State
Anderson	2015	Movement, Navigation Capacity, Internal State Space Use, Internal State, External Fac-
Anguiano	2015	tors, Movement, Motion Capacity

Bailey	2011	Survival,External Factors
Baxley	2009	Space Use,External Factors
Baxley	2016	Movement,Internal State,External Factors
Barazowski	2016	Space Use,Thecnical
Bauder	2012	Movement,Space Use,Motion Capacity
Bauder	2019	Space Use,Movement,Internal State,External Factors
Bauder	2015	Movement,Space Use,Internal State,
Baxley	2011	Space Use,External Factors
Beapure	1995	Space Use,External Factors
Beck	1995	Space Use,External Factors,Internal State
Bell	2007	Space Use,Movement,External Factors
Bertram	2001	Space Use
Bertram	2001	Space Use
Blouin-Demers	2007	Movement,Space Use,Internal State,Motion Capacity
Blouin-Demers	2000	Space Use,Internal State
Blouin-Demers	2001	Space Use,External Factors
Blouin-Demers	2002	Space Use,External Factors,Internal State
Blouin-Demers	2003	Movement,Internal State,External Factors
Breiningner	2012	Survival,External Factors
Brown	1976	Motion Capacity,Internal State,Space Use
Brown	1976	Movement,Space Use,Internal State,External Factors
Brown	2009	Movement,Navigation Capacity,External Factors
Brown and Whitehead	1999	Space Use,Internal State,External Factors
Brown and Whitehead	2000	Movement,External Factors,Internal State
Bryan	2015	Space Use,Internal State Space Use,Motion Capacity,Internal State,External
Buchanan	2017	Factors
Burger and Zappartoli	1998	Space Use,External Factors
Carfagno	2006	Space Use,External Factors,Internal State Motion Capacity,Space Use,External Factors,Internal
Carrasco-Harris	2020	State
Carter	2012	Space Use,External Factors
Charland	1995	Movement,Space Use,Internal State
Chase	2017	Space Use,External Factors,
Clark	2005	Motion Capacity

Clark	2006	Movement,External Factors
Cobb	2005	Movement,Internal State,External Factors,
Coupe	2002	Movement,Internal State
Crane	2008	Space Use,External Factors
Cross	2015	Space Use,External Factors
De Gregorio	2011	Space Use,Movement,Internal State
De Gregorio	2014	Tenical
De Gregorio	2015	Movement,External Factors
Degregorio	2017	Movement,Space Use
Densatis	2019	Tenical
Diffendorffer	2005	Movement,Internal State,External Factors,Space Use
Dodd E Barichivich	2007	Movement,Space Use
Dugan	2016	Space Use,External Factors
Durbian	2008	Space Use,Internal State
Ealy	2004	Movement,External Factors
Fill	2015	Space Use,External Factors Movement,Motion Capacity,Space Use,External Fac-
Flaherty	2020	tors
Fortney	2020	Space Use,External Factors
Galigan	1979	Motion Capacity
Gardiner	2015	Space Use,External Factors
Gardner-Santana	2009	Movement,Space Use,Internal State
Garfagner	2009	Space Use,Movement,External Factors Movement,Space Use,External Factors,Internal
Gerald	2006	State,Motion Capacity
Godwin	2011	Movement,Space Use
Goetz	2016	Movement,External Factors
Gomez	2015	Movement,Navigation Capacity,External Factors
Goulet	2015	Space Use,External Factors
Graves	1993	Space Use,Navigation Capacity,Internal State
Halstead	2019	Movement,Space Use,External Factors
Halstead	2009	Space Use,Movement,External Factors
Hart	2015	Space Use,Motion Capacity,External Factors
Harvey	2006	Space Use,External Factors
Harvey	2011	Movement,External Factors

Harvey	2014	Movement
Heres	2018	Space Use,External Factors
Himes	2001	Space Use,External Factors,Internal State
Hinderliter and Lee	2004	Space Use,External Factors,Movement
Hoss	2010	Space Use,External Factors
Howey	2016	Space Use,Movement,External Factors,Internal State Movement,Motion Capacity,External Factors,Space
Howze	2012	Use
Howze	2015	Space Use,Movement,External Factors,Internal State
Howze	2012	Movement,External Factors
Hyslop	2014	Space Use,External Factors,Internal State
Hyslop	2012	Movement,External Factors,Internal State
James	2013	Tenical
Jellen	2014	Movement,Internal State
Jellen	2007	Movement,Space Use,Internal State
Jones	2013	Survival
Johnson	2000	Space Use,Motion Capacity,Internal State
Jungen	2019	Tenical
Kapfer	2008	Movement,Space Use,Internal State
King	2004	Survival,Space Use,External Factors
Kingsbury	2000	Space Use,External Factors
Kjoss	2001	Space Use,External Factors
Klug	2011	Motion Capacity,Space Use,Movement
Klug	2010	Space Use,External Factors
Lagory	2009	Space Use,External Factors
Larsen	1987	Space Use,Movement,External Factors
Leuemberger	2019	Movement,Internal State,External Factors
Linehan	2010	Space Use,Internal State
Lomas	2019	Movement,Space Use,External Factors
Macgowan and Walker	2013	Space Use,Movement,External Factors
Magg	2017	Space Use,Internal State,External Factors
Martino	2011	Space Use,Movement,External Factors,Internal State
Mata-Silva	2015	Space Use,Movement,Motion Capacity
Mata-Silva	2018	Space Use,Movement
McInnes	2013	Space Use,Space Use

Mead	2018	Space Use,Internal State,Motion Capacity
Mead And Stark	2018	Space Use,External Factors,Internal State
Michael	2013	Movement,Space Use,External Factors,Internal State
Miesma	2011	Space Use,Internal State
Miler	2012	Space Use,External Factors,Internal State,Space Use
Mitrovich	2009	Movement,Space Use,External Factors
Mitrovich	2018	Movement,Space Use,External Factors,Internal State,
Mohr	2012	Movement,Internal State
Moore	2006	Space Use,Motion Capacity,External Factors
Moriarty	1991	Movement,Space Use,Internal State,External Factors
Mullin Et Al	2000	Space Use
Murray	2010	Space Use,External Factors
Nelson	2000	Movement,External Factors
Nodberg	2017	Movement,External Factors
Nodberg	2016	Movement,External Factors
Nowak	2002	Motion Capacity,Space Use,External Factors
Oldham	2016	Movement,Internal State
Olson	2015	Survival,Internal State,External Factors
Parent E Whitehead	2000	Movement,Internal State,External Factors
Parker E Anderson	2007	Movement,Space Use,Internal State,External Factors
Patten	2016	Motion Capacity,Space Use,Movement,Internal State
Petersen	2019	Movement,Space Use,Internal State
Plumer	2020	Space Use,Movement
Price	2014	Movement,Space Use,External Factors
Prior	1996	Space Use,External Factors
Radke and Walkom	2008	Movement,Space Use
Reinert	1998	Movement,Space Use,Internal State,External Factors
Reinert	1999	Movement,Space Use,External Factors
Reinert	1984	Space Use,Internal State,External Factors
Richardon	2006	Movement,Space Use,External Factors,Internal State
Robson	2013	Movement,External Factors,Internal State
Roe	2003	Movement,Space Use,Internal State
Roe	2010	Movement,Space Use,Internal State,External Factors
Roth	2005	Space Use,Internal State
Roth	2011	Movement,Internal State,External Factors

Roth	2005	Space Use,External Factors,Internal State
Rouse	2011	Movement,Internal State
Row	2006	Space Use,External Factors
Rudolph	1997	Space Use,External Factors
Sacerdote-Velat	2014	Space Use,Movement,External Factors
Sawyer and Baccus	1996	Space Use,Movement,External Factors
Scheutt	2012	Space Use,Movement,Internal State,
Sealy	2002	Space Use,Movement,Navigation Capacity
Secor	1994	Space Use,Movement,External Factors,Internal State,
Secor	1995	Movement,Space Use,Internal State
Shepherd	2008	Movement,External Factors
Shine	2000	Movement,Internal State,External Factors
Shine	2001	Movement,Space Use,Internal State,External Factors
Siegel	2002	Movement,Internal State,External Factors
Smith	2015	Movement,External Factors
Smith	2017	Tenical
Smith	2018	Tenical
Smith	2009	Movement,Space Use,External Factors,Internal State,
Smith	2015	Space Use,Internal State
Sperry	2008	Space Use,External Factors
Sperry	2009	Movement,Internal State,External Factors,Survival
Sperry	2010	Movement,External Factors,Survival
Sperry	2012	Movement,Internal State
Stanford	2010	
Steen	2009	Space Use,Internal State
Steen	2013	Movement,External Factors
Tezlaff	2017	Movement,Internal State,External Factors Space Use,Internal State,Movement,External Fac-
Timmerman	1995	tors,Motion Capacity
Titus	2007	Movement,Internal State,External Factors
Vanek and Wasko	2017	Space Use,External Factors
Wagner	2014	Space Use,External Factors
Waldron	2008	Space Use,External Factors
Waldron	2013	Movement,External Factors
Walters	2016	Space Use,External Factors

Ward	2013	Tenical
Wasko	2009	Space Use, Movement, External Factors, Internal State
Wasko	2010	Space Use, Internal State, External Factors
Wastel	2011	Movement, Space Use, Internal State
Wastell E Mcenssy	2016	Movement, Space Use, Internal State, External Factors
Weatherhead	1985	Space Use, External Factors
Weatherhead	2010	Movement, External Factors
Weatherhead	1989	Movement, External Factors
Weatherhead	2012	Movement, External Factors
Williams	2015	Space Use, External Factors, Internal State
Williams	2012	Movement, Space Use, External Factors
Wills	2000	Movement, External Factors
Wilson	2018	Space Use, External Factors
Withing	1997	Space Use, Movement, Internal State, External Factors
Withing	1996	Movement, External Factors
		Movement, Space Use, External Factors, Internal
Wunderle	2004	State, Motion Capacity
Wylie	2010	Space Use, External Factors
Wylie	2011	Tenical
Yagi	2020	Movement, Space Use, External Factors
Zappartoli	2011	Space Use, External Factors, Movement
Zappartoli	2015	Motion Capacity, Internal State, External Factors
Chiaravigilo	2006	External Factors, Internal State
Quintana	2017	Space Use, Internal State, External Factors
Rivas	2016	Motion Capacity, Space Use, Internal State
Rodrigues-Pedraza	1998	
Smaniotto	2020	Space Use, Motion Capacity
Tozetti	2009	Movement, Space Use, Internal State, External Factors
Tozetti	2013	Movement, External Factors, Internal State
Crane	2016	Space Use, External Factors
		Space Use, External Factors, Movement, Motion Capac-
Crysti	2017	ity
Daltry	1998	Movement, Space Use, External Factors, Internal State
Ettling	2013	Space Use, Movement, Internal State
Jung-Yung	2009	Movement, Space Use, External Factors, Internal State

Kans	2002	Movement,Space Use
Karn	2000	Movement,Motion Capacity,Space Use Movement,Navigation Capacity,Internal State,External
Kojima	2014	Factors
Lee Et Al	2009	Space Use,Internal State
Marshal	2019	Movement,Space Use
Rao	2013	Movement,Space Use,External Factors
Rhaman	2014	Space Use,External Factors
Shine	2003	Space Use,Movement,Internal State,External Factors
Staner	2015	Tenical
Strine	2018	Space Use,Movement,External Factors
Voris	1996	Movement,Motion Capacity,External Factors
Blàzquez	1995	Movement,Motion Capacity,Internal State
Brito	2003	Movement,External Factors,Internal State
Hand	2019	Movement,Space Use,External Factors,Internal State
Kovar	2016	Space Use,External Factors
Lelièvre	2010	Space Use,Internal State,External Factors
Marinez-Freiria	2018	Space Use,Movement,External Factors
Mertens	1994	Movement,Motion Capacity,External Factors Motion Capacity,Space Use,External Factors,Internal
Nash and Griffiths	2018	State
Neuman	2011	Space Use,Motion Capacity
Nilson	1999	Space Use,Internal State,External Factors
Reading	2009	Space Use,External Factors

Appendix 4 – Papers used to classify species

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Appendix 5 – Quantity of papers for species

Specie	quantity
<i>Crotalus horridus</i>	26
<i>Sistrurus catenatus</i>	20
<i>Pantherophis obsoletus</i>	19
<i>Coluber constrictor</i>	10
<i>Nerodia sipedon</i>	9
<i>Pituophis melanoleucus</i>	9
<i>Morelia spilota</i>	8
<i>Pituophis catenifer</i>	8
<i>Agkistrodon contortrix</i>	7
<i>Crotalus adamanteus</i>	7
<i>Drymarchon couperi</i>	7
<i>Heterodon platirhinos</i>	7
<i>Masticophis flagelum</i>	7
<i>Crotalus atrox</i>	6
<i>Thamnophis sirtalis</i>	6
<i>Crotalus oreganus</i>	5
<i>Agkistrodon piscivorus</i>	4
<i>Pituophis ruthveni</i>	4
<i>Python bivittatus</i>	4
<i>Sistrurus tergeminus</i>	4
<i>Acrocordus arafurae</i>	3
<i>Boiga irregularis</i>	3
<i>Crotalus viridis</i>	3
<i>Lampropelis Getula</i>	3
<i>Liasis fuscus</i>	3
<i>Pseudonaja textilis</i>	3
<i>Thamnophis gigas</i>	3
<i>Bitis gabonica</i>	2
<i>Bothrops asper</i>	2

<i>Chilabothrus innornatus</i>	2
<i>Crotalus cerastes</i>	2
<i>Crotalus durissus</i>	2
<i>Crotalus lepidus</i>	2
<i>Elaphe schrenckii</i>	2
<i>Farancia abacura</i>	2
<i>Natrix natrix</i>	2
<i>Nerodia erythrogaster</i>	2
<i>Nerodia harteri</i>	2
<i>Ophiophagus hannah</i>	2
<i>Pantherophis emori</i>	2
<i>Pseudechis porphyriacus</i>	2
<i>Regina septemvittata</i>	2
<i>Rhabdophis tigrinus</i>	2
<i>Vipera berus</i>	2
<i>Zamenis longissimus</i>	2
<i>Zamenis scalaris</i>	2
<i>Achantophis praelongus</i>	1
<i>Boa Constrictor</i>	1
<i>Bogertophis subocularis</i>	1
<i>Bungarus candidus</i>	1
<i>Calloselasma rhodostoma</i>	1
<i>Chilabothrus subflavus</i>	1
<i>Crotalus helleri</i>	1
<i>Crotalus molossus</i>	1
<i>Crotalus ruber</i>	1
<i>Crotalus tigris</i>	1
<i>Dolichophis jugularis</i>	1
<i>Emydocephalus annulatus</i>	1
<i>Enhydris enhydris</i>	1
<i>Eunectes beniensis</i>	1
<i>Eunectes murinus</i>	1
<i>Eunectes notaeus</i>	1
<i>Farancia erythrograma</i>	1
<i>Fordonia leucobalia</i>	1

<i>Gloydus shedaoensis</i>	1
<i>Gloydus ussuriensis</i>	1
<i>Heterodon simus</i>	1
<i>Hierophis viridiflavus</i>	1
<i>Hoplocephalus bungaroides</i>	1
<i>Hoplocephalus stephensi</i>	1
<i>Hypsicopus plumbea</i>	1
<i>Lampropelis californiae</i>	1
<i>Lampropeltis caligaster</i>	1
<i>Lampropeltis triangulum</i>	1
<i>Lichanura trivirgata</i>	1
<i>Macroptera lebetinus</i>	1
<i>Malpolon monspessulanus</i>	1
<i>Masticops lateralis</i>	1
<i>Montivipera raddei</i>	1
<i>Morelia viridis</i>	1
<i>Natrix tessellata</i>	1
<i>Nerodia fasciata</i>	1
<i>Nerodia taxispilota</i>	1
<i>Notechis scutatus</i>	1
<i>Opheodrys vernalis</i>	1
<i>Pantherophis guttatus</i>	1
<i>Pantherophis sp</i>	1
<i>Pseudonaja affinis</i>	1
<i>Senticolis triaspis</i>	1
<i>Sistrutus Miliarius</i>	1
<i>Stegonotus cucullatus</i>	1
<i>Thamnophis saurita</i>	1
<i>Trimeresurus macrops</i>	1
<i>Vipera latastei</i>	1

CONCLUSÃO

A grande maioria dos trabalhos com ecologia do movimento de serpentes ao redor do mundo segue a mesma receita, investiga a relação do movimento ou uso do espaço com alguma variável relativa a sua causa ou consequência, sem aprofundar a discussão para as repercussões ecológicas a nível de indivíduo, população, comunidade ou ecossistema. Além disso estão mais concentrados na região dos Estados Unidos da América com algumas poucas espécies da família viperidae e colubridae sendo muito estudadas enquanto a grande maioria das espécies aparece em apenas um ou dois artigos. A espécie mais comum em estudos de ecologia do movimento é *Crotalus horridus* na América do norte.

A grande maioria dos estudos estudou a influência de fatores externos e internos no movimento e uso do espaço das serpentes, no entanto poucos artigos estudaram capacidade locomotora e capacidade de navegação das serpentes, ainda menos estudaram a relação do movimento com a sobrevivência, sucesso reprodutivo, competição intra e interespecífica e sua influência na dinâmica da população, comunidade e ecossistema.

O movimento das serpentes não é aleatório, serpentes se locomovem de maneira a conseguir os recursos necessários a manutenção de sua vida e evitar condições potencialmente perigosas. Também acompanham as variações sazonais na disponibilidade de recursos e mantem sua área de vida em volta de abrigos onde possam passar o período de digestão, descanso ou hibernação. Abrigos de boa qualidade são usados novamente e em alguns casos compartilhados com outras serpentes, outras espécies de répteis e até anfíbios.

Os padrões de movimento e uso de espaço das espécies de serpente, não sofrem grande influência das relações filogenéticas, apesar de alguns grupos específicos como os viperideos, partilharem uma influência considerável de seu parentesco. Estes padrões são mais fortemente influenciados por características individuais como tamanho, sexo, idade, e período reprodutivo, e por características comuns a toda a espécie como modo reprodutivo, período

de atividade e tipo de ambiente onde vivem. Esperamos que este trabalho ajude a avançar as fronteiras do nosso conhecimento sobre comportamento e ecologia de serpentes