



DEPARTMENT OF BIOLOGICAL AND
ENVIRONMENTAL SCIENCES

Understanding the movement of Peringuey's adder in the Namib Sand Sea

With the use of radio telemetry and temperature
data



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Abstract

This study aimed to increase the knowledge of the viperid Perringuey's adders (*Bitis peringueyi*) movement by examining if there is a connection between minimum nightly temperature, length of an individual and distance travelled in a straight line. Understanding movement of a species is important since it both describes current behavior and aids in understanding how changes to the environment affect the species. The adder is highly specialized to the extreme environments of the sand dunes in the Gobabeb area in the northernmost part of the Namib sand sea. Establishing a baseline of knowledge is very important as both increasing temperatures from climate change could impact the health of either or both the species and the ecosystem in the future. Data was gathered by tracking, capturing and tagging individuals then using radio telemetry to track their movements through the environment once per day as well as collecting weather data from Gobabeb weather station. The data was then put through a generalized linear mixed model with different environmental and individual variables in order to assess how they impacted the snake's movements. Results gained from the study were not statistically significant, but there were weak negative associations between distance travelled (straight line distance) and both minimum nightly temperature and individual length. There is a high probability this is a result of the limited number of individuals that could be tagged due to logistic constraints. If a suggestion of a conclusion is to be drawn from the data, it is that there is an adaptation for using hotter nights to hunt for more active ectothermic prey, that would result in a lesser movement as the species is a sit and wait predator. However expanding the study with more individuals and over a larger timeframe is necessary to confirm or deny these findings.

Key Words: Radio telemetry, Movement ecology, Namib desert, Perringuey's adder, *Bitis peringueyi*

Introduction

The study of animal movement and the impact of terrain

Movement ecology is a central topic when trying to understand the behavior of species both relative to one another as individuals as well as interaction with other species and the environment around them. Tracking animals comes with possible gains of knowledge in several areas. It is often used for understanding what habitats animals prefer, home range size, how and to where they migrate and how genes flow within populations (Angelici et al., 2000; Maritz & Alexander, 2012a, 2012b; Nordberg et al., 2021; Sector, 1994). By tracking species at several locations or over a larger time frame it is also possible to understand behavioral change based upon abiotic factors such as temperature or altitude or biotic factors such as mating or how predators and prey interact (Angelici et al., 2000; Maritz & Alexander, 2012a, 2012b; Nordberg et al., 2021; Sector, 1994). As an example Angelici et al. (2000) followed gaboon vipers by tracking animals following implanting Very High Frequency (VHF) transmitters and noting the environments and activity of the snakes. They found what habitats were preferred and how time was spent doing different activities.

Movement becomes especially important when observing nature in a conservational setting, it is very important to know how an animal behaves in order to properly protect it (Nordenberg et al., 2021; Wilmers et al., 2015). Nordenberg et al. (2021) tracked Timber rattlesnakes in fragmented protected areas and found that their protection was not adequate and the snakes often wandered outside the protected area. Critically, Nordenberg et al. (2021) also found what paths they utilized. Information that, in the future can be referenced when creating new protected areas so that they properly protect more species.

Movement ecology is also an important factor for when addressing how species might be affected by changing climate, both Maritz and Alexander (2012b), Harvey and Lersen (2020) as well as Sector (1994) found when studying three different species of snakes, that temperature and seasonality affected how far and where snakes moved so a changing climate will most likely affect the movement as well. A change in movement is not necessarily confined to one species because one species movement can affect another (Wilmers et al., 2015). When Wei et al. (2025) studied the relationship between active hours of two small rodents and two predators they saw that not only did the predators' active hours mimic their prey but also avoided each other.

Study species

The Peringuey's adder

The Peringuey's adder (*Bitis peringueyi*) is a snake endemic to the sandy dunes of the Namib sand sea. Morphologically they are small snakes most commonly with a Snout Vent Length (SVL) between 20-25cm but up to over 30cm in some cases (African Snakebite Institute, n.d.; Broadley, 1983). Colouration is pale yellow to chestnut brown, they have patterns of dark and light dots and dotted lines along their backs, the tail is three out of four cases similarly coloured and in the rest a darker black colour (Broadley, 1983; Robinson & Hughes, 1978; Figure 1B). Their eyes are the most noticeable and recognizable trait as they are uniquely located on top of their head instead of on the sides to aid while hunting (African Snakebite Institute, n.d; Broadley, 1983; Robinson & Hughes, 1978; Figure 1B).

The Peringuey's adder is a sit and wait predator, burrowing just under the sand surface leaving only the tops of their heads exposed while waiting for prey to wander close enough to strike, their prey consists of different dune-living reptiles (African Snakebite Institute, n.d; Broadley, 1983; Holm & Sholtz, 1980; Robinson & Hughes, 1978).

The Peringuey's adder is also locally known as the Sidewinder, it gets this name from the stereotypical movement that the snakes use to traverse the dunes. Sidewinding is a way of propulsing itself that is thought to be more effective for snakes to use when moving over flat smooth surfaces. The movement consists of keeping two points of contact with the ground while lifting the rest of its body away from the surface of the sand, almost leaping forwards with the head before making a new point of contact. Unlike

other snakes who use both sides of their body to push off obstacles, when the snake sidewinds only one side of the body is used to push on the surface of the ground itself. This sidewinding movement results in very characteristic tracks that are not connected to one another (Figure 1A). The tracks vary in angle depending on if the snake is ascending a slope, when they will be almost horizontal (Jayne, 2020; Figure 1A). If moving over a flat surface or descending a slope they will be more angled forwards (Jayne, 2020).

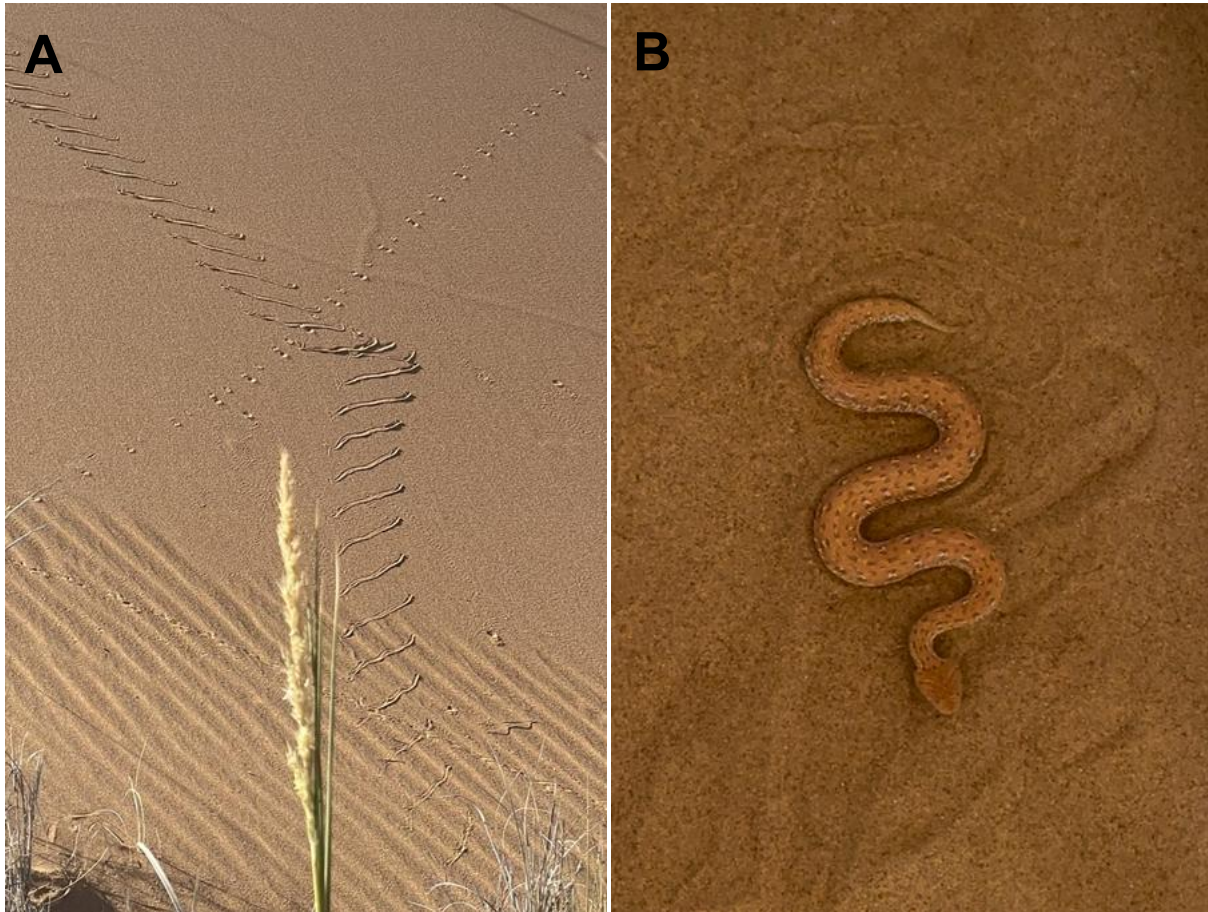


Figure 1, A, Tracks from Perringuey's adder ascending a dune. B, A Perringuey's adder

It is mentioned by several sources that individuals with a black tail will sometimes leave the tail exposed while burying, and then use it to lure prey closer (African Snakebite Institute, n.d.; Broadley, 1983; Holm & Sholtz, 1980), although it seems as this behaviour has only ever been seen utilized by a single individual held in captivity at Gobabeb Namib research institute and without any photographic evidence. Most sources (Broadley, 1983; Holm & Sholtz, 1980; Robinson & Hughes, 1978) also mention that the Perringuey's adder will harvest fog from the air to condense as droplets of water on their body. Then guiding the water to their head by positioning their body like a funnel (Holm & Sholtz, 1980), then again raising their head to allow for swallowing (Broadley, 1983; Holm & Sholtz, 1980; Robinson & Hughes, 1978). This behavior can also be questioned as the original source only mentioned that the snakes lick water droplets from their body when sprayed with fine mist, not funneling it (Louw, 1972). These two last examples show that the little that is known about Perringuey's adder's behaviors might be victim to exaggeration from previous sources and these claims are commonly spread.

Lack of knowledge

Researching the Perringuey's adder sheds light upon a major lack of previous research. Most information is from a single description of the animals (Robinson & Hughes, 1978) where one pregnant female was caught and she and her young were observed in captivity during a time. Then there are mentions of the species with limited, often singular anecdotal observations in other papers on the general area (Holm & Sholtz, 1980; Louw, 1972). There are also a couple of studies handling the genetic relations of the genera where

the species is mentioned but there is no mention of their behaviour (Calvete et al., 2007; Wittenberg et al., 2015). There is especially a lack of studies on this unique, very specialized snakes behaviour in the wild. As one of the largest predators in the area research is needed, this lack of research was highlighted by Henschel and Lancaster in 2013 when reviewing studies done in the area during 1962-2012. They point out the need for research to be done with models for large scale ecosystem dynamics as well as the nutrient pathways in the ecosystem and the ecology of endemic or range restricted species (Henschel & Lancaster 2013). It is important to remember that a large reason for the lack of knowledge for specifically African snake ecology is that there is a lack of both interest and funds compared to snakes from other areas of the globe (Maritz & Alexander, 2012a, 2012b; Angelici et al., 2000).

Comparable species

Namaqua Dwarf adders

A very close relative to the Perringuey's adder is the Namaqua Dwarf adder (*Bitis schneideri*) (Wittenberg et al, 2015). The species hunt and live in very similar ways although the Namaqua Dwarf adder is slightly smaller, and they inhabit different dune habitats. The Namaqua Dwarf adder resides in smaller coastal dunes with a high vegetation coverage and the Perringuey's adder residing in large dunes with a very low to moderate vegetation coverage (Maritz & Alexander, 2012b; Robinson & Hughes, 1978). When studies were done by Maritz and Alexander (2012a, 2012b) on the movement of the Namaqua Dwarf adder using radio telemetry it was found that the adder does not move very far, only averaging between three and six m for both male and female individuals with one exception. During springtime and mating season males tended to move a lot further, about 50m every day, this was thought to be because the males were searching for a mate.

North American Sidewinder

A genetically unrelated but movement-wise similar snake that might give an insight into the movement of Perringuey's adder is the North American Sidewinder (*Crotalus cerastes*). The species is often about double the length of most Perringuey's adders with a mean SVL of 49.5cm and differ behaviorally as it migrates to overwinter in borrows and hunts more actively (Secor, 1994) The species is like the Perringuey's adder also known for sidewinding as an adaptation to moving over loose sand. When studied by Sector in 1994 he revealed that they move large distances, the mean movement was ca 95m (straight line distance) and the maximum distance covered by one individual was 902.6m during one single night. This study has some methodological differences when compared to the similar study by Maritz and Alexander (2012). Where Maritz and Alexander (2012) tracked the movement only in straight lines from where they had found the snakes, meaning that they did not measure the path and true distance traveled. Sector (1994) followed the tracks as well as took a straight line distance from starting to stopping point.

Aim

The aim of the study was to gain an understanding of the movement of the Perringuey's adder based upon different environmental and morphological variables. By tracking VHF tagged snakes and relating daily movement patterns to biometric and environmental data.

Material and method

Study location

The study location was the central northern border of the Namib sand sea in the Namib Naukluft national park, specifically the area around Gobabeb research institute on the dune named Station dune (23° 33' 37.1"S 15° 02' 25.4"E; Figure 2). This area is characterized by large dunes stretching in a north south direction with large areas of interdunal planes (Holm & Scholtz, 1980). The dunes are made up of different habitat types easily identified by plant coverage and the structure of the sand (Holm & Scholtz, 1980). At the bottom of each dune is the dune slope, categorized by a large number of small to very large hammocks of different species and a relatively low incline (Holm & Scholtz, 1980; Figure 4). The most common hammock species on the dune slope is the Namib dune bushman grass (*Stipagrostis sabulicola*) followed by the !Nara melon (*Acanthosicyos horridus*) (Holm & Scholtz, 1980; Figure 4). These plants create habitats by stabilizing the sand, providing shade as well as harvesting coastal fog that gives the area its main source of water (Holm & Scholtz, 1980). When continuing up the dunes, plant cover almost disappears completely as the slipface and crest of the dune is reached (Holm & Scholtz, 1980). The slipface and crest make up one side of the dune each, as the wind packs sand on one side creating the relatively stable crest, the slipface is created on the other side of the dune with looser sand (Holm & Scholtz, 1980; Figure 5). Although there is little vegetation far up the dune there are many different burrowing animals who during the peak hours of day take refuge underneath the sand such as the shovel-snouted lizard (*Aporosaura anchieta*) (Holm & Scholtz, 1980). The area is hyper arid and receives extremely little precipitation every year (Rohde et al, 2019). Namibia at large has been receiving less rainfall and more extreme temperatures during the last decade which might increase aridness (Kwembeya & Shikangalah, 2023). Although during the last 100 years there has been an increase in plant coverage in the area around Gobabeb and fog seems to be stable or increasing with more extreme oceanic temperatures even in recent times (Rohde et al., 2019). This means an increase in precipitation unlike the rest of Namibia.

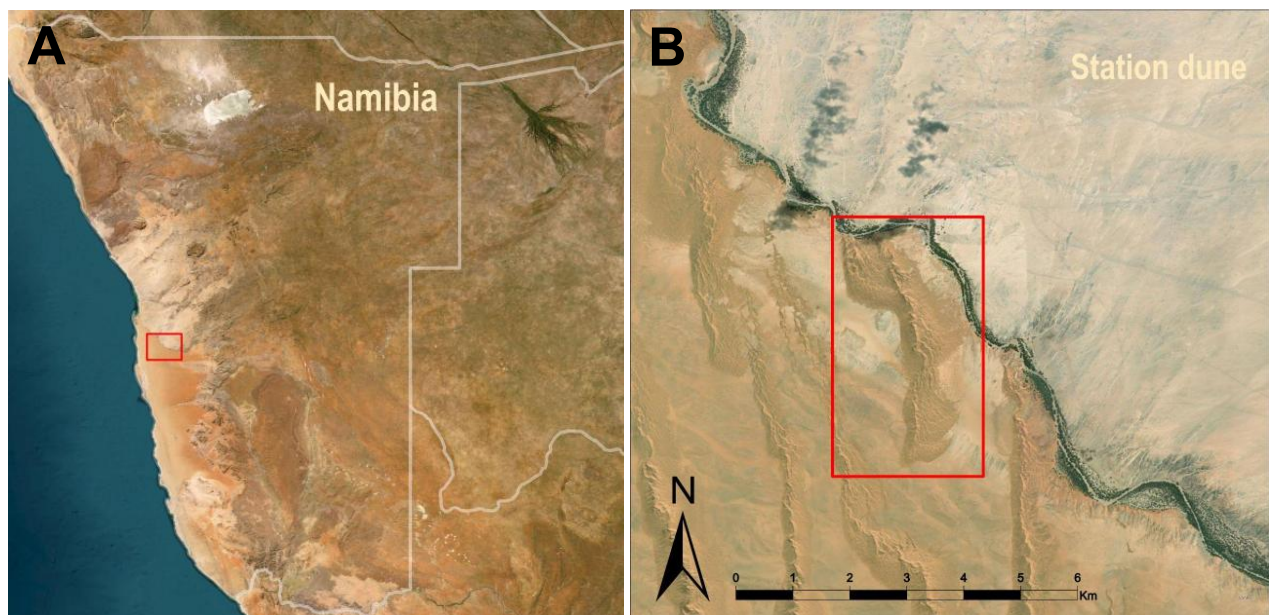


Figure 2. A, Location of study area in Namibia. B, Location of the dune named Station dune in the Gobabeb area.

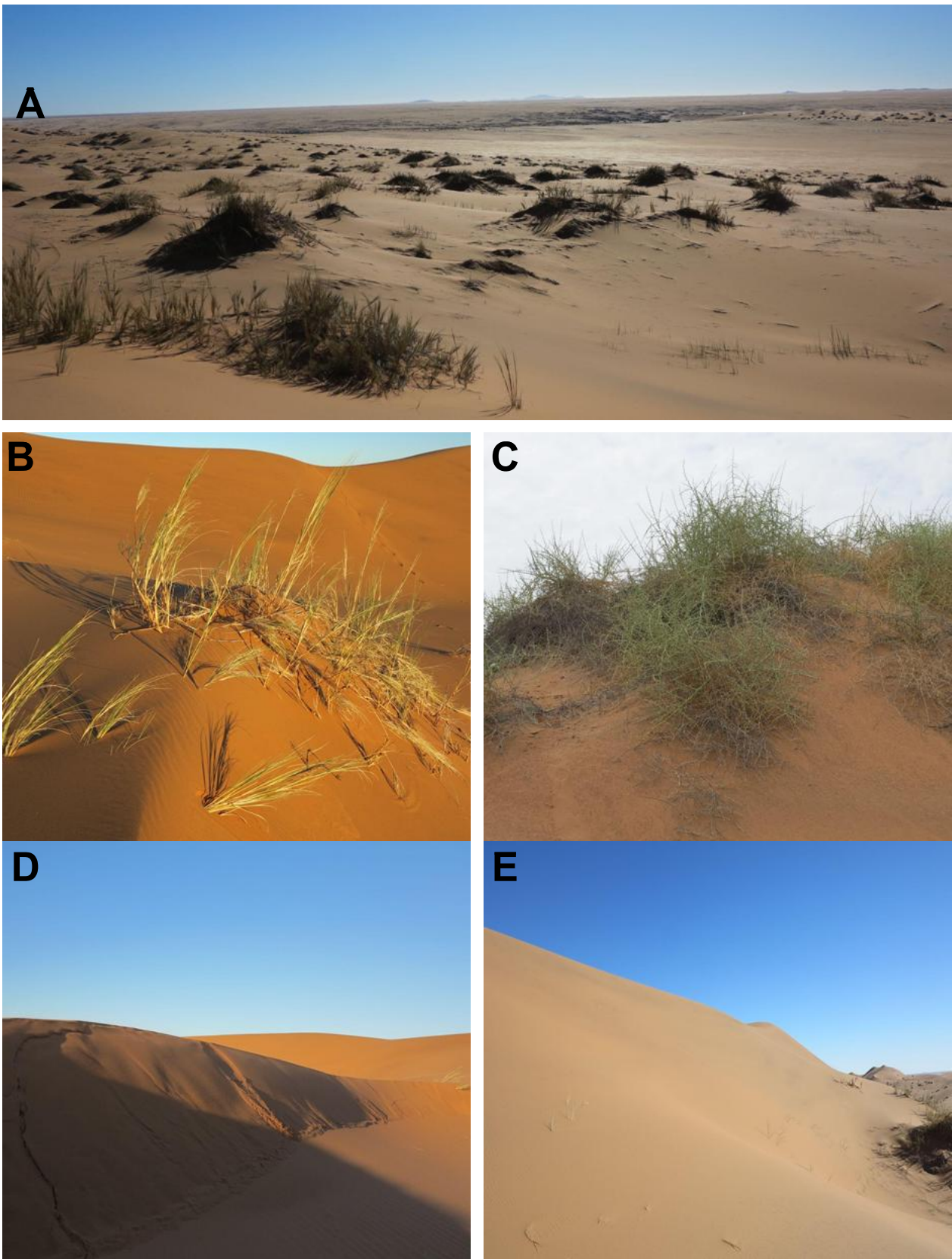


Figure 3. **A**, Dune slope with varying sizes of hammocks. **B**, Hammock of Namib dune bushman grass. **C**, Hammock of !Nara melon. **D**, Dune slipface with very loose sand. **E**, Dune crest with stable windblown sand.

Capture and Tagging

The Peringuey's adder was captured by searching the dune slopes in the early morning when the wind was calm, preventing tracks being blown away from the nightly movement and the sun easing the tracking by casting shadows. To cover the large distance of the dune, a quad-bike was driven along the dune slipface. The slipface was the most surveyed area because of the soft sand that results in the snakes leaving deeper tracks that are easier to spot, when a track was spotted it was followed on foot. When tracking a handheld GPS device was used to record the routes (Garmin eTrex 10), however this data was not used in the final model as the original position of the snake was not found. If an individual was found it was captured by hand using leather gloves and then transferred to a cloth bag. After capturing an individual, it was taken back to Gobabeb for weighing and measurement of SVL. Weight was done by first measuring the snake in the bag used for capturing, then re-measuring the bag after transferring the individual to a terrarium. While measuring SVL it was a goal to do it as least intrusively as possible using an online tool (Wilton-Jones, 2025). The online tool is used by photographing a snake on a flat surface with a ruler, then comparing a line of a known length along the ruler, to one shaped along the length of the snake (Wilton-Jones, 2025). The snakes were kept at Gobabeb inside individual terrarium with availability for shelter both by burying and by hiding in grassy substrate. Each individual was kept for as short a time as possible but due to unforeseen disturbances in global shipping the time spent in terrariums was unfortunately increased. VHF transmitters weighing approximately 1g (Advanced Telemetry Systems, A1055) were then attached to the snakes with a cyanoacrylate adhesive slightly posterior of the mid body on the dorsal side of each individual (Figure 6). The attachment was done by constricting an individual with gloves then pressing a transmitter with adhesive on the dorsal side until it had hardened completely. The weight of the transmitters was limited to 1g to stay under 5% of the bodyweight of the snake in order to minimally affect the tagged individual while still providing data during an appropriate time. After attaching the transmitters, it was made sure that each snake could move freely and bury completely including the transmitter, before being released within 24 hours of tagging.



Figure 4. Peringuey's adder with VHF transmitter (Advanced Telemetry Systems, A1055) attached

Daily Tracking and Distance data

The study tracked each snake every morning by driving a quadbike to their last known location. When arriving at the location it was first checked if the individual had moved at all. Simply checking for a signal at

the exact location as the day before using a 3-element yagi antenna and a Communications Specialist R1000 handheld receiver proved if it was still there. If the signal seemed to have moved the first attempt of tracking was done by checking for track to follow. If tracks were found they were followed by foot and mapped using a handheld GPS, while simultaneously checking signal strength as to not accidentally disturb a buried snake. The tracks were followed until the snake was found again and the route was saved. If tracks were not found the snake was instead located directly via VHF telemetry as done by Maritz and Alexander (2012a, 2012b). When a snake was located in this way a route was not recorded but instead a waypoint was recorded as the new location.

The distances were not measured in the field, rather the GPX-files that were acquired were converted into features and then measured in ArcGis pro (Esri, 2024). This was done by first using the GPX to features tool, then distances were measured using the measure distance tool from the last known location to the new location (Esri, 2024).

Temperature data

The temperature data for the ambient temperature was collected through the regular work of the Gobabeb Namib research institute's weather station, which collects ambient temperature every hour. The minimum temperature each night was chosen to represent each movement because this was thought to be more impactful on an ectotherm's movement than maximum nightly temperature.

Data analysis

To test the hypothesis that the movement of Perringuey's adder is affected by with either minimum nightly temperature and/or SVL a generalized mixed linear model was used with a tweedie error distribution. The model included straight line distance as the dependent variable and independent variables of SVL and minimum nightly temperature, snake ID was used as a random effect. The tweedie error distribution was chosen in order for the model to handle an expected right skewed distribution that included distances of zero.

Permits

The study followed Gobabeb research institute's ethics panel, which is reviewed by the Namibian Ministry of Environment, and in turn follows international ethics common in most universities for animal ethics. The work was done under the research permits of the Gobabeb research institute.

Results

Capture, Attachment and daily tracking

The initial tracking and capturing went on for about two months and resulted in movement data from three individuals. The attachment of VHF transmitters itself went well however during the time of tracking the individuals, transmitters fell off several times. Once both the adder and trackers were found and it could therefore be reattached but in the other cases the individual was not found again. The method of following tracks almost had to be abandoned due to wind conditions throughout the time after the trackers were attached except the first day. This resulted in almost only straight lines being measured and not the true distance an individual travelled during a movement and therefore a lot less accurate distances.

Movement

The average daily movement measured was about 8m (7.94m, SD±4.51m). The analysis of the data shows a weak negative correlation between both minimum nightly temperature and SVL with movement (minimum nightly temperature: -16% (95% CI: -38% to +28%), $p > 0.50$; SVL: -26%, (95% CI: -42% to +35%), $p > 0.45$; Figure 7 & 8), meaning when a snake was longer or temperatures were higher the individuals tended to move less. The random effect of snake ID resulted in a varying intercept close to zero (random effect variance < 0.001).

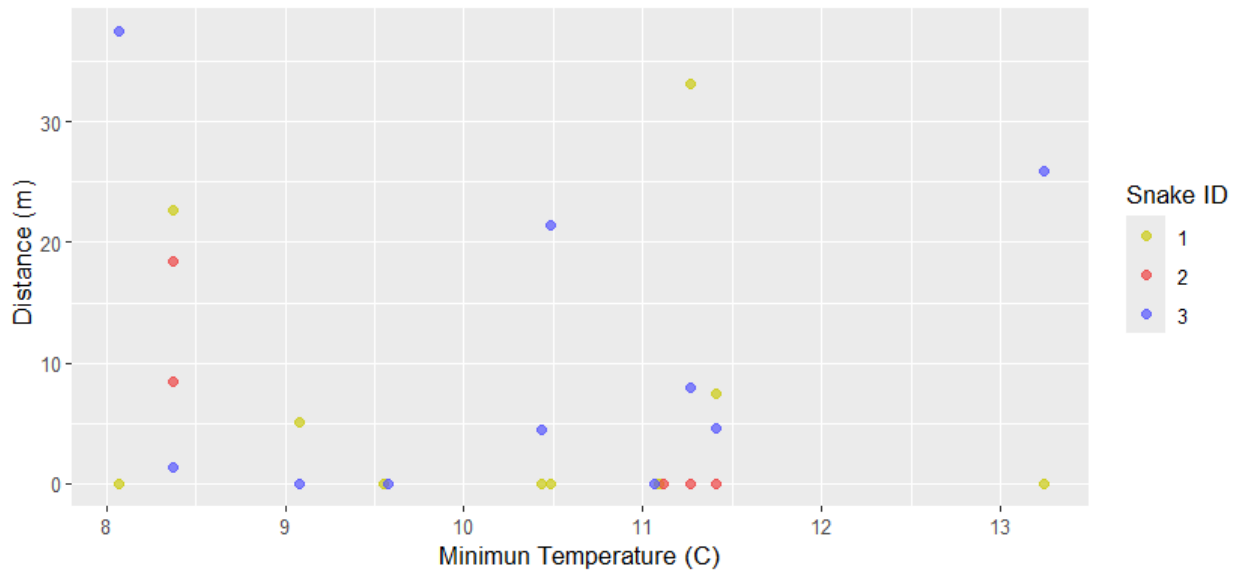


Figure 5. Showing minimum nightly temperatures plotted against the distance traveled in a straight line by an individual during one night. Points with the same value were displaced horizontally using the beeswarm package to better show the distribution.

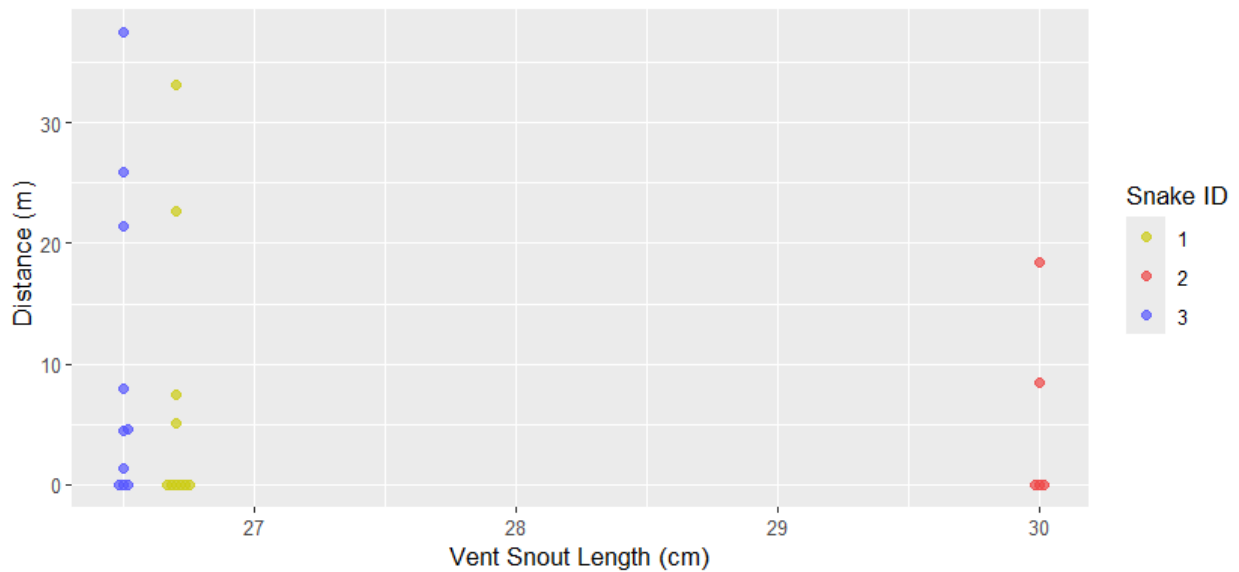


Figure 6. Length between vent and snout plotted against the distance traveled in a straight line by an individual during one night. Points with the same value were displaced horizontally using the beeswarm package to better show the distribution.

Discussion

Movement

Compared to similar species

The Peringuey's adder moves around more than its close relative of South Africa. The mean distance measured during the study was almost 8m, and although it is quite low the furthest distance a Peringuey's adder moved was more than 460m. This distance was measured when following an incomplete track during the capturing phase of the study, therefore the true maximum distance is further. The Namaqua Dwarf adder had a mean movement between 3-6m and a maximum movement of just 140m (Maritz & Alexander, 2012a). This is quite similar and could be because of the close genetic relationship, as well as the two species sharing quite similar habitats and practically identical hunting strategies (Alexander & Maritz, 2012a, 2012b; Robinson & Hughes, 1978). But the Namaqua dwarf adders' smaller size and more vegetated environment could be a good explanation for the slightly shorter distances. It is worth mentioning that the movement of the Peringuey's adder was measured during autumn, but the movement of the Namaqua dwarf adder was measured during all seasons except autumn (Maritz & Alexander, 2012a, 2012b).

The average movement of the Peringuey's adder does not compare to the North American sidewinder, who moved a mean of almost 95m in a straight line as an adult (Secor, 1994). More than 10 times the mean measured for the Peringuey's adder. When comparing the maximum distance covered the North American sidewinder travels only about double that of the Peringuey's adder with 902.6m (Secor, 1994). This seems to show that when the Peringuey's adder moves far, it is proportionally a lot further than the North American sidewinder. It has to be remembered that the North American sidewinder doubles the average SVL of a Peringuey's adder and also hunts differently which might explain the differences (African Snakebite Institute, n.d.; Broadley, 1983; Secor, 1994)

Minimum temperature

Because of the statistical uncertainty it is impossible to either reject or accept a correlation of the minimum temperature and straight line movement. The statistical uncertainty stems from having very few individuals and to a lesser degree because data was gathered during a short time. Much more data would be needed to claim an understanding of the relationship between straight line movement and minimum nightly temperature. Therefore it is only possible to make suggestions of why a relationship between increasing minimum temperature and straight line movement would be negative. A theory proposed by Wei et al. (2025) is that there is a relationship between a predator's movement and movement activity of its prey. Because the Peringuey's adder preys upon ectotherms and uses a sit and wait hunting strategy. It might be suggested that they utilize warmer minimum temperatures when prey is more active for hunting, and would therefore sit still on these nights. Instead using colder nights when prey is less active to move.

Snout vent length

When addressing the relationship between SVL and straight line movement, the small sample size is even more influential since the study only has three SVL values to predict values from. Additionally, two of the SVL were very similar. Because of this no relationship between SVL and straight line movement can be concluded from this study

Random Variable inclusion

The gathered data resulted in a practically non-existent random effect variance for the snake ID. When confronted with such a low random effect variance it might rightfully be questioned why it was not removed from the model or switched to a fixed effect in favor of simplification. This study chose to keep Snake ID in as a random effect because it is the biologically correct thing to do. In a scenario where more individuals would have been included it would have been beneficial to be included as a random effect in order to shrink the distribution of errors and better explain variation (Boller et al, 2009).

Limitations and Future studies

Limitations and improvements

Several limitations about this study were learned that might be used to improve future studies of either the same species or species with similar ecology. Driving a quadbike along the slipface, trying to spot and follow tracks was, due to environmental conditions often very ineffective. In order to find tracks that could be followed to an individual over both soft sand and more compact sand very fortunate wind conditions with low wind during nighttime that did not pick up during morning was required. If wind speeds went over ca 6m/s it was practically impossible to see tracks other than on the slipfaces where the sand is the softest. These tracks could therefore not be followed to a snake. To counteract this one could either simply look for individuals during a different time of year, possibly during the Spring as their closest relative is most active then (Maritz & Alexander, 2012b). Alternatively, it was noted how the snakes are attracted to shadows when temperatures are high and will approach them to seek shelter. Based upon this behaviour snakes might be attracted to bury at certain places by creating artificially shaded areas.

Using shade traps could also deal with a possible problem with bias. In this study only snakes that at least once traveled on the slipface were caught, because further down on the dune slope or on the dune crest tracks were incredibly hard to spot. However, these snakes might not be representative of the population at large. If shade traps were used they could be placed evenly over a dune and hopefully capture a more representative part of the population.

As mentioned before the transmitters fell off several times during the study. There is no mention of this happening in the previous study on the Namaqua Dwarf adder (Maritz & Alexander, 2012a, 2012b). Why this happens is probably a mix of different environmental factors such as high and highly variable temperatures. But as these environmental factors are impossible to avoid I would consider trying the method done on the North American Sidewinder in future studies where trackers were instead surgically implanted (Sector, 1994). Although this would require the aid of a veterinarian or similarly trained individual and thorough ethical review as it is extremely invasive.

Observations for future studies

Interesting observations made that would warrant more study is that, the North American sidewinder was noted to use serpentine locomotion before switching to sidewinding in the beginning of a movement, thought to warm up the muscles (Secor, 1994). No Pinguicula's adder did this either when observed in the wild or in captivity, they seemed to strictly use sidewinding to move itself other than when moving through hammocks or large amounts of grassy substrate where it would switch to climbing through the vegetation. There was one exception to this, when in captivity and moving very slowly along the glass they seemed to utilize rectilinear locomotion, something other species of the genus quite commonly does but has not been noted for the Pinguicula's adder before. Understanding these differences might help us understand why one species evolved in a certain way and what specific condition caused it

Another note about the movement of the adders was that they were often (a clear majority of the time) observed or tracked to ascend up a side of the dune either completely or a majority of the way then travel a short distance horizontally and then descend the same side. Why this highly energy draining movement would occur is unclear. Understanding why this is done could aid in expanding knowledge in how snakes choose where they move and what senses they use when picking a route.

During the rain events of early April two snakes caught with 2 weeks difference but otherwise kept in the same conditions shed within 24 hours of each other. Although this is only one observation, it would be interesting to research if water availability or possibly an increase in humidity might trigger these snakes to shed. Many snake species require water for proper shedding for both the process but also because they lose water while shedding. Because of this, an adaptation to shed when moisture is available is in my opinion not unreasonable. If this was further researched, it could help predict how a lack or increase in water availability might affect both Pinguicula's adder and similar snakes around the globe.

Conclusion

This study investigated if distance moved in a straight line is correlated with minimum nightly temperature or SVL for the Peringuey's adder. A negative trend was found in both cases however it was weak and non-significant, therefore no conclusion could be drawn. This does not mean a correlation does not exist, simply that it cannot be proven or disproved with this data. I propose that the negative trend between temperature and distance reflects a real negative effect of temperature on distance moved, because of the preferred hunting style and prey of the Peringuey's adder. I suggest that Peringuey's adder sits still during warm nights when their prey is more active in order to hunt using their borrowing strategy and would therefore use colder nights to move when hunting chances would be worse. Further work with a larger sample of individuals as well as understanding the activity of the prey is needed. In addition, it was noted that the Peringuey's adder moved more than the Namaqua Dwarf adder and less than the North American sidewinder. This is thought to be because of the difference in habitat, size and hunting style. When comparing it was found that the average movement was more than its relative but a lot less than the North American sidewinder. When comparing maximum distance noted the Peringuey's adder traveled a lot further than the Namaqua Dwarf adder, and over halfway of the much larger North American sidewinder's maximum movement.

Finally, it was concluded that the method for this study could be greatly improved by alternative and potentially more efficient capture and tagging methods. For example, using shade to induce burrowing at certain locations and using surgically implanted tags.

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