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Habitat selection during movement pathways in the
Aesculapian snake (*Zamenis longissimus* (Laurenti,
1768)) in its introduced range in Colwyn Bay, North
Wales.

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Supervisor: Wolfgang Wüster

Key Words: *Zamenis longissimus*, Non-native, Habitat selection, Radio-tracking, Integrated
Step Select Functions

Authors declaration

'Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy. Rwy'n cadarnhau fy mod yn cyflwyno'r gwaith hwn gyda chytundeb fy Ngoruchwyliwr (Goruchwylwyr)

'I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards. I confirm that I am submitting this work with the agreement of my Supervisor.'

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Abstract

Non-native species can significantly impact novel environments. Ecological studies that include a species' movements in its habitat can inform management and policy decisions for the control of introduced species. Information learned can be used to identify movement pathways and habitat preferences to predict dispersal routes and limitations for range expansion. Understanding which environmental features influence movement can lead to more successful control and targeted removal. Native to southern and central mainland Europe, the Aesculapian snake (*Zamenis longissimus*) was introduced into the UK twice; during the 1960s in North Wales then later in the 1980s in London. The population in Colwyn Bay, North Wales is the northernmost extant of their range. Previous studies of northern populations in their native range have identified preferences for anthropogenic features and woodland, but we know very little about which habitat features are selected during movement. However, few studies investigating snake movement ecology include habitat selection during movement but rather focus on where a snake starts moving and then the location and habitat in which it settles. This study used radiotelemetry to locate adult male snakes between May and August 2022 in a largely suburban and agricultural landscape. We radio-tracked a total of seven snakes five times each day over this period to identify habitat preferences along movement pathways. Locating focal snakes enabled us to observe individual behaviour to gain insight into the distances moved but also into how snakes exploited habitat features available to them. Using Integrated Step Select Functions (ISSF), we analysed how habitat features influenced movement.

Habitat features had no influence on the step characteristics (step length and turning angles of observed locations) but were affected by the distance of an observed step towards a habitat feature. We found at the population level snakes were positively associated with hedgerows, buildings, and scrub. High levels of variability toward habitat selection between individuals show a level of habitat generalism. Similar to other reptile species, *Z. longissimus* also exhibits a high degree of individual heterogeneity, further complicating predictions for movement.

However, linear features including hedgerows were frequently used as pathways through the fragmented landscape. The findings of this study highlight the importance of understanding movement ecology in non-native snake species. Using preferences for habitat features, especially along pathways can inform decisions on where is best to focus for targeted searches or to place traps for future removal if necessary. This will increase the probability of snake detection and capture rates, also aiding in reducing the associated costs and labour requirements. With increased global connectivity and climate change, this population should continue to be monitored into the future to respond quickly to any changes including range expansion.

Introduction

Movement is a fundamental process essential to the fitness and survival of an animal. As an essential behaviour in the life history of an individual, it is the result of a continuous decision-making process in terms of how, when, and where to displace. The reasons for movement can vary across the lifetime of the individual with age, sex, and reproductive status influencing their movement patterns (Holyoak *et al.*, 2008; Nathan *et al.*, 2008; Karelus *et al.*, 2017). Environmental factors can also contribute to the decision on where and why an individual moves. Less suitable environments and increased competition can affect movement rates leading to reduced fitness of a population (Nathan *et al.*, 2008). Factors including climate change, anthropogenic modifications, and introduced species disrupt and alter the movement patterns of animals.

Non-native or introduced species, are animals that exist outside of their naturally occurring range (Ricciardi and Cohen, 2007). The impacts of most non-native species are largely unknown, often with little to no documented impact (Jeschke *et al.*, 2014). Most fail to persist outside of their natural range but populations that can survive are typically small and isolated (Ricciardi, 2016; Tedeschi *et al.*, 2021). However, the success of an introduced organism can vary between species, regions, and entire ecosystems (Buckley and Catford, 2015). An introduced species can become invasive when it becomes established (Blackburn *et al.*, 2011). To be defined as invasive there must be a rapid range expansion following its introduction outside of its natural range, consistent breeding success (self-replacing population), and it must be responsible for negative impacts on the environment, the economy, or health (Yan *et al.*, 2001; Pyšek *et al.*, 2020; Polce *et al.*, 2023). Invasive species are a large threat affecting biodiversity (Roy *et al.*, 2014). Worryingly, the rates of biological invasions have increased significantly since the 1970s (Walther *et al.*, 2009). Invasive species may have few limiting factors such as natural predators or competition for resources in their introduced range (Polce *et al.*, 2023). Correlations between the presence of invasive species and ecological impacts have been recorded, examples include population declines and local extinctions (Cuthbert *et al.*, 2021).

Adaptations in response to a non-native species can be slow resulting in a higher risk of population declines and extinction especially if already vulnerable (Lettoof *et al.*, 2023). This is concerning for specialist or endemic species that have adapted to fit specific niches for instance habitat or dietary requirements (Lee *et al.*, 2019). Endemic species have evolved without competition, or defence against novel predators and parasites or diseases (Silva-Rocha *et al.*, 2022). There is the potential for introduced species to be vectors for diseases and parasites (Pauwels and Pantchev, 2018). Native species can experience negative impacts affecting their abundance and behaviour, contributing to population isolation, home range contraction, hybridisation, and genetic bottlenecking with fewer breeding individuals (Pyšek *et al.*, 2020; Feuka *et al.*, 2022). Early detection and a quick response to the presence of a non-native species is essential as once invasive species have become established successful eradication can be difficult. Steele (2023) reviewed the success and failure of twenty eradication case studies in Florida. Over half of these case studies resulted in a successful outcome. However, this varied between taxa; there was no documented success in the removal of invasive herpetofauna. One example was the black spiny-tailed iguanas (*Ctenosaura similis*) on Gasparilla Island. Despite significant efforts between 2008 and 2011 and the removal of over 9000 individuals, this species continues to persist in several counties and removal efforts have slowed (Steele, 2023; Avery *et al.*, 2014).

Introductions of non-native or invasive species can be either deliberate or accidental from a variety of different routes that include anthropogenic corridors and unaided spread from previously introduced areas. The escape or release from captivity is the most common introduction pathway for vertebrate species (Pyšek *et al.*, 2020). Many of the methods for introduction are of anthropogenic origin, and the ease of importing and buying exotic plants and animals has likely contributed to increased numbers. Established non-native vertebrate species in Europe have increasingly derived from the pet trade, and modifications to legislation for the importation and possession have been used to mitigate potential introductions from high-risk species (Keller *et al.*, 2011). Despite this, non-native species have spread globally with increased human expansion and improved global connectivity with many of these species connected to human-dominated environments (Baxter-Gilbert *et al.*, 2021).

A higher tolerance of people and other sources of human disturbance enables species to live alongside humans in anthropogenic environments or urban niches (Lowry *et al.*, 2012). Keller *et al.* (2011) highlighted species existing in human-dominated environments are more likely to become invasive. Living near humans can provide benefits from human-subsidised resources equating to greater food availability, fewer natural predators, to the use of anthropogenic shelters that offer security and warm conditions (Lowry *et al.*, 2012). The ability to adapt to change will determine survival success (Lowry *et al.*, 2012).

Selection pressures in these environments can help drive rapid evolution causing behavioural and morphological adaptations (Borden and Flory, 2021). As an example, cane toads (*Rhinella marina*) have invaded multiple countries to date including Australia causing severe issues since their introduction. Studies on their invasive populations have recorded rapid evolution for instance behavioural and physiological changes, habitat selection of novel environments, and morphological differences (Rollins *et al.*, 2015; Baxter-Gilbert *et al.*, 2021). Hudson *et al.* (2020) described cane toads that were making larger moves on the edges of their non-native range as having longer legs, increasing their dispersal rates.

The establishment of alien reptile species globally remains low; one assessment by Dawson *et al.* (2016) found the percentage of established plants, mammals, and birds was higher than reptiles. However, islands and coastal locations are disproportionately likely to host novel reptile species (Dawson *et al.*, 2017; Capinha *et al.*, 2017; Pyšek *et al.*, 2020; Maestresalas *et al.*, 2023). A successful invasion is largely dependent on life history traits and the effort of the initial introduction; higher efforts from multiple locations will increase the likelihood of establishment and range expansion (Daly *et al.*, 2023). Allen *et al.* (2017) investigated the relationship between fast life histories and the success of invasive reptiles and amphibians. Reptile species with larger, more frequent clutches and shorter reproductive lifespans were traits frequently associated with established and spreading populations (Allen *et al.*, 2017; Street *et al.*, 2023). Fast life history traits allow small, introduced populations to increase rapidly. This reduces the time a

population is vulnerable to random events such as individual deaths, disease, or fluctuations in environmental conditions (Allen *et al.*, 2017).

Squamates (the order that contains snakes and lizards) are more frequently invasive when compared to other herpetofauna (Capinha *et al.*, 2017). The potential impact of invasive snake species can have long-lasting and irreversible impacts. Cases of well-known non-native snake species are brown tree snake (*Boiga irregularis*), which decimated local bird and reptile populations in Guam (Rodda and Fritts, 1992; Gibbons *et al.*, 2000; Wiles *et al.*, 2003), and the Burmese python (*Python bivittatus*) in Florida has had severe adverse impacts on the ecosystem including severe population declines of mammal species (Dorcas *et al.*, 2012; Wilson, 2017). More recently the Horseshoe whip snake (*Hemorrhoids hippocrepis*) and California kingsnake (*Lampropeltis californiae*) are thought to be linked to declines in native reptile populations (Montes *et al.*, 2021; Piquet and López-Darias, 2021, Piquet *et al.*, 2021). The Brahminy blind snake (*Indotyphlops braminus*) has the potential for quick range expansion due to its parthenogenic reproductive strategy which contributed to their successful introduction to over fifty countries (Faraone *et al.*, 2019). However, despite its wide introduced range the impacts of this species are still unknown.

Early detection in reptiles and more specifically snakes can be difficult due to their cryptic nature and life history traits and once established, eradication is often unsuccessful (Feuka *et al.*, 2022). Reptiles are frequently traded globally as part of the exotic pet trade; escape or release from captivity has been the suspected cause of many invasive reptile species. However, many of these escaped or released individuals are unlikely to become established due to environmental constraints. Tropical regions are often more susceptible to invasions from non-native species as they provide more suitable conditions (Feuka *et al.*, 2022). Establishment is more likely if an introduced range has similar climate conditions to its native range (Filz *et al.*, 2018). Ectothermy can be advantageous in these environments for introduced reptiles, removing the constraints of using food to produce heat and allowing opportunistic strategies to adjust to novel environments (Allen *et al.*, 2017). Warmer

ambient temperatures and less defined seasons, for example, breeding timings aid in rapid population expansion and dispersal.

Northern climates may prove harder for invasive herpetofauna to establish due to a reliance on external climatic conditions including temperature for thermoregulation, breeding, egg development and incubation, reduction in active time before hibernation, and potential movement restriction (While *et al.*, 2015; Claunch *et al.*, 2021). Global climatic shifts may impact colder climates, where previously species that were unable to establish could become capable of breeding or expanding current introduced ranges with increased temperatures (Walther *et al.*, 2009; Boyle *et al.*, 2016). Climatic warming might increase the frequency of introductions and establishment (Walther *et al.*, 2009). Predictions for the future indicate increased temperatures and more frequent weather events such as severe droughts. Howell *et al.* (2021) suggested non-native species may favour drier hydrological conditions whereas native species may not have the ability to adapt.

The United Kingdom (UK) has an issue with numerous high-profile invasive species becoming established, examples include the North American signal crayfish (*Pacifastacus leniusculus*), American mink (*Neovison vison*), and Japanese knotweed (*Fallopia japonica*) (Holdich *et al.*, 2014; Martin and Lea, 2020; Martin *et al.*, 2020). Stroh *et al.* (2020) reported that the distribution and abundance of non-native plants have increased and surpassed the number of native species in the UK and Ireland. The UK non-native species secretariat (NNS, 2023) has identified over 2000 non-native species present in the UK with up to 15% of these species having the potential to become invasive in Britain. The number of species with the potential to invade has not depleted so the probability of more species becoming established in the future is entirely possible (Seebens *et al.*, 2017). Currently, the UK has three documented breeding (or established) non-native reptile species (Manchester and Bullock, 2001). Other species have been reported, usually either escaped individuals or small non-breeding populations with most being extremely localised (Langton *et al.*, 2011). Reproductive success has been documented in the western green lizard (*Lacerta bilineata*), wall lizard (*Podarcis muralis*), and the Aesculapian snake (*Zamenis longissimus*) (Mole, 2010; Langton *et al.*, 2011).

The Aesculapian snake (*Zamenis longissimus* (Laurenti, 1768)) is a European colubrid reaching an average length of 1.5m, with some southern European individuals reaching a maximum length of just over 2m (Edgar and Bird, 2006). They are fairly slender snakes with relatively long tails in comparison to their total length and have angled ventral scales to aid with climbing. This species is non-venomous using constriction to kill its prey and is regarded as a generalist predator. Most of their diet is made up of mammals but can also include birds (eggs and nestlings), reptiles, amphibians, and invertebrates in juvenile snakes (Capizzi *et al.*, 2008; Lelièvre *et al.*, 2012a; Najbar, 2007). Mating typically occurs between May and June, with females typically laying up to eighteen eggs around the end of June to July (Edgar and Bird, 2006; Speybroeck *et al.*, 2016). Hibernation occurs between September and March depending on the location, northern populations may need to hibernate for longer periods.

The Aesculapian snake has a wide distribution throughout Europe, particularly Central and Southern Europe including Spain, Italy, Greece, France, Slovenia, Russia, Iran, Turkey, and the Czech Republic. Small, isolated populations exist in Poland, Sardinia, Georgia, and Germany (Speybroeck *et al.*, 2016). These isolated populations are often restricted to specific locations due to particularly favourable conditions. Isolated populations on the northern edges of their geographic distribution remain from a wider distribution in a warmer climate during the Holocene (Musilová *et al.*, 2007). During the mid-Holocene when temperatures were higher, *Z. longissimus* had a distribution as far north as Denmark until the 19th century before their localised extinction (Allentoft *et al.*, 2018). Fossil remains have also been discovered in Suffolk and Essex, England, providing evidence of their presence in the UK (Holman, 1994; Musilová *et al.*, 2007). Their range has reduced and shifted south due to climate temperatures cooling leaving isolated populations particularly vulnerable. At least five isolated populations have gone extinct, including the population in Denmark going extinct in the late 19th century and Switzerland around the 1970s (Allentoft *et al.*, 2018; Musilová *et al.*, 2010).

In the UK, there are two confirmed separate populations. The first established population of *Z. longissimus* in Colwyn Bay, North Wales, is currently the

northernmost of their entire extant range. This population originated from the Welsh Mountain Zoo between the late 1960s and early 1970s. A former Welsh Mountain Zoo employee described the location and how *Z. longissimus* were housed in two old Victorian greenhouses. After their removal, juvenile *Z. longissimus* were found around the grounds in the 1970s. That was the first indication that one or multiple snakes had escaped but the exact circumstances are unknown. This non-native snake species is successfully breeding in the UK, but their range over the last sixty years has remained localised to the zoo and the immediate surrounding areas. The second established population is located around Regent's Canal in Camden, London, where they are often encountered along the banks. This population was first discovered in the 1980s its origins are unknown but is thought to have either escaped from a nearby education centre or been released by unknown individuals (Langton *et al.*, 2011). This population has also had success in breeding, both adult and juvenile snakes have been recorded, but the size of the population is unknown.

As a widespread European species, *Z. longissimus* has been studied extensively with research into their dietary composition (Luiselli and Rugiero, 1993; Naulleau and Bonnet, 1995; Capula and Luiselli, 2002; Najbar, 2007; Lelièvre *et al.*, 2012a), thermal biology (Lelièvre *et al.*, 2012b; Lelièvre *et al.*, 2010), spatial ecology (Luiselli and Capizzi, 1997; Lelièvre *et al.*, 2012b; Kovar *et al.*, 2016a; Kovar *et al.*, 2016b), and population ecology (Kovar *et al.*, 2014; Kurek *et al.*, 2017; Kurek *et al.*, 2019). All current information on the ecology of *Z. longissimus* has been from their native range. Previous radiotelemetry studies for this species have either included a small sample size of snakes or an infrequent radiotracking schedule. Kovar *et al.* (2016) investigated habitat use in populations of *Z. longissimus* at two sites in northwest Bohemia, tracking six snakes; however, tracking was infrequent with snake locations recorded once or twice a week. In another study, three snakes were radio-tracked in Bohemia to investigate the population's behaviour and temperature when close to roads, each snake had less than thirty fixes (Kovar *et al.*, 2014). These studies investigated habitat preferences at a landscape and microhabitat level in northern isolated European populations.

Lelièvre *et al.* (2010) and Lelièvre *et al.* (2012b) both included larger samples of thirty and thirty-two individuals respectively, tracked every forty-eight hours during their active period (between May and September) over one year. Although these studies used radiotelemetry procedures for their data collection, the former explored thermal strategies and energetics (thermoregulation, thermal preferences, sensitivity of locomotory performance and metabolism) and the latter movement patterns and home range sizes. Lelièvre *et al.* (2012b) found most snake relocations were less than 100m and only two observations were over 600m, and males moved more frequently than female snakes. The non-native UK Species Secretariat has *Z. longissimus* recorded but is lacking in information. The dispersal mechanisms, management, and impact of this species in the UK are unknown. There is currently no other published research available, therefore, we know very little about their behaviour and habitat selection.

Considering that studies have indicated native and introduced animals can behave differently from each other we have a substantial knowledge gap. Different selection pressures from their core range can lead to variation in activity levels, behaviour for instance increased boldness and aggression (Lowry *et al.*, 2012; Baxter-Gilbert *et al.*, 2021), and the use or attraction to novel features and habitat. Movement ecology is one important factor when considering the best approach to impede the spread or removal of an introduced population. The relationship between an introduced species and its novel environment is integral to the creation and advancement of management strategies (Nafus *et al.*, 2018; Batoszek *et al.*, 2021). Understanding the environmental constraints affecting the survival of a non-native species is an important factor to consider and is often neglected, few studies have used radiotelemetry to understand reptile movement ecology in the UK. In their native range, *Z. longissimus* is known to occupy a variety of different habitats depending on their location and all movement ecology knowledge comes from their native range. This presents an issue when determining the best approach to control the existing populations in the UK. Radiotelemetry can reveal aspects of spatial ecology which include the ability to navigate its environment, home range size, movement patterns, and details of habitat use (Batoszek *et al.*, 2021).

Limited research is available on snake habitat selection while moving; habitat selection studies primarily focus on stationary selection overlooking information to establish movement pathways and potential dispersal routes. Studies that focus on habitat selection while moving are seldom done in reptiles. Consequently, important behavioural interactions within novel environments could be missed along with the choice of which habitat structures are used for traversal, or which are avoided during bouts of movement. For the control of introduced species, this is a lost opportunity to reduce the accessibility of corridors limiting their dispersal potential.

Aims and Hypotheses

This is the first study to examine the movement ecology of Aesculapian snakes (*Zamenis longissimus*) in the UK using radiotelemetry, and the first to use methods that incorporate integrated step selection functions (ISSF) which compares used against available locations to explore the relationship between movement and habitat selection. By studying their choice of pathway selection, we investigated what drives their decision-making, which in turn could indicate potential dispersal routes and barriers for this population. We aimed to investigate the relationship between movement patterns and habitat selection in their introduced range in Colwyn Bay, North Wales to provide recommendations for the control or removal of this non-native population.

Here we use radio telemetry of *Z. longissimus* to address the following questions:

(1) Which habitat features present in the environment will snakes select to use along movement pathways? (2) Do Aesculapian snakes display avoidance of any habitat features that may act as a dispersal barrier? And (3) are the distances *Z. longissimus* moves influenced by their selection of habitat features?

Methodology

Study site

The study site covers an area of approximately 1.7km² (see Figure 1) located between two towns, Colwyn Bay and Mochdre, North Wales, and the immediate surrounding area (53.28 to 53.29°N, -3.74 to -3.76°W). The area contained a mosaic of habitats, comprised of mostly anthropological and agricultural features. Consequently, the study site included sections of both towns which were comprised of housing, caravan parks, and industrial areas. The area is composed largely of meadows and pastures with the fields enclosed and separated by hedgerows. Most pastures are grazed infrequently by sheep and cattle, towards the end of July and August many of these fields went under rotational grazing by livestock (cattle) or mowing with the vegetation being removed. The site also includes the Welsh Mountain Zoo which covers an area of 0.15km² and contains around 100 different species. Large sections of the zoo are therefore inaccessible due to animal enclosures and other manmade structures and buildings. The zoo draws in around thousands of visitors a year with the summer months being the busiest. The zoo grounds are also well maintained with consistent gardening and landscaping. Most of the animal faecal matter and vegetation waste goes to a large compost pile in the southeastern corner of the zoo, which has been a suspected location for females to lay their eggs. Eggs have been discovered in the pile, which is one of the areas where neonate snakes appear first. Patches of deciduous forest and small patches of gorse scrub are scattered over the entire study site, a small patch of woodland opposite the Zoo was in the process of development and was being removed. Roads are found throughout the entire site, with busy roads surrounding the zoo and the connecting meadows and pastures, with a dual carriageway (A55) being a major roadway to the North (Figure 1).

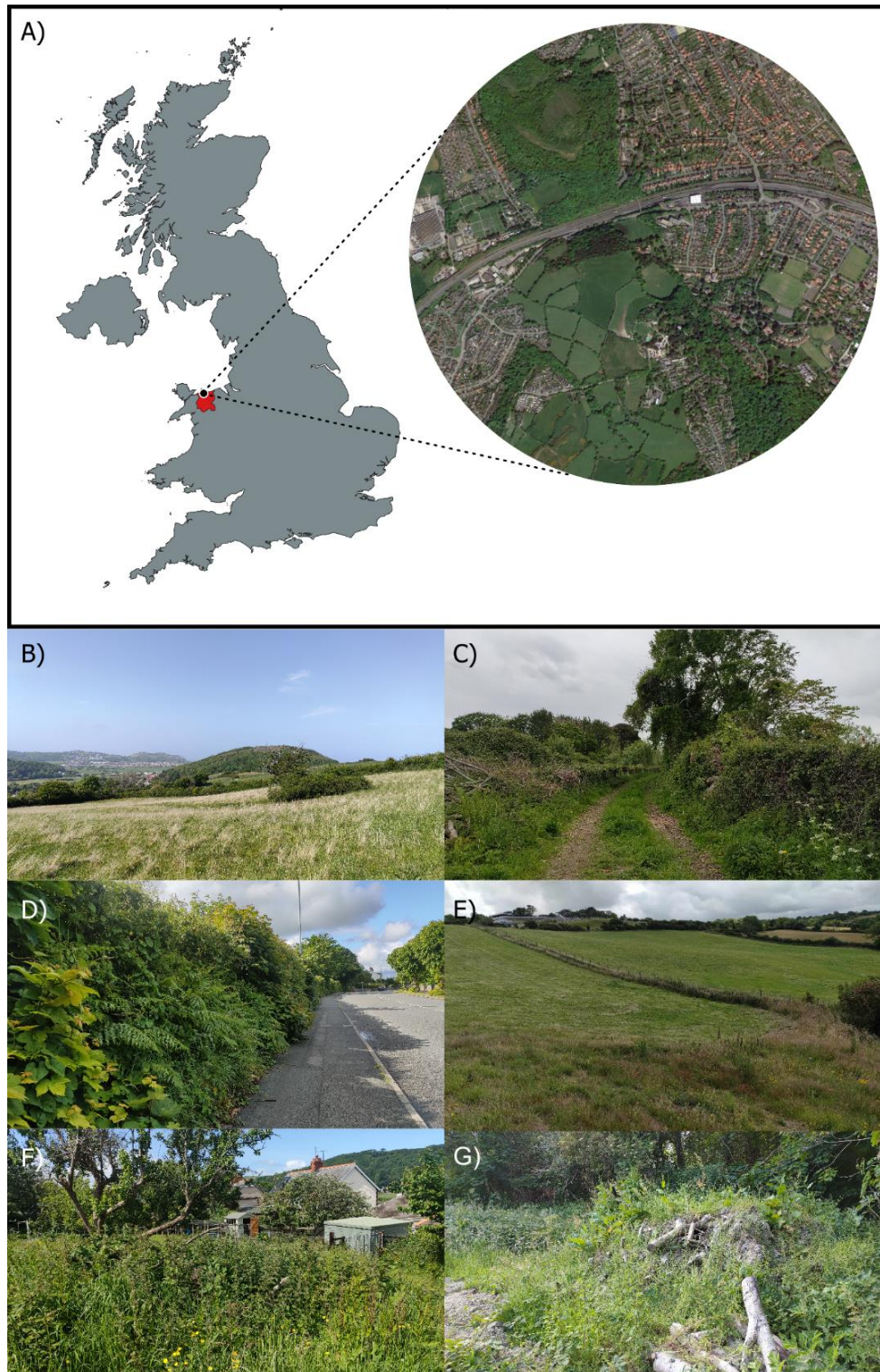


Figure 1. A) Map showing the location of the study site in Colwyn Bay, North Wales in relation to the UK. B) – G) are examples of locations where tracked snakes were recorded in the environment. Map created in QGIS Desktop v3.26.2 (<https://qgis.org/>) with Google satellite.

Snake capture, processing, and surgery

The cryptic nature of snakes and the secretive behaviour of *Z. longissimus* caused difficulty in finding suitable snakes early enough to track for the duration of their active season. Snakes were caught during visual surveys, opportunistically by zoo employees, or from notifications by residents between April and August 2022. The surveys included checking refugia (roofing felt 1m x 1m and 30cm x 30cm), log piles, and compost heaps along set survey routes. Snake captures were non-random, presenting the possibility of bias in our sample. Only male snakes were selected because of the differences in movement distances and frequency between the sexes. This decision was based on past literature: previous studies found male snakes move more frequently providing us with the necessary sample size needed to run the analysis, as thoroughly sampling one sex was preferable to a poor sample of both (Lelièvre *et al.*, 2012b). The use of male *Z. longissimus* was also advantageous because on average home ranges are larger and during the breeding season males travel further when actively mate searching, making them more suitable when studying movement and dispersal capabilities (Edgar and Bird, 2006; Lelièvre *et al.*, 2012b). Male snakes were more available than females early in the season because of mate searching behaviour, providing more opportunities for capture. Male individuals were therefore able to be tracked earlier in the season and for a longer duration.

When a snake was captured, we recorded the time, date, location, and temperature. We recorded the snout-vent length (SVL cm), tail length (TL cm), weight (g), bolus (presence of items in the midgut), sex, and age class. Photos of the head, dorsal, tail, subcaudal, and other characteristic features (scarring, fused scales, injuries, or disease) were taken as records. Dietary information was taken as part of another study into the population ecology. Individuals were given a unique ID (ZALO###) and given a PIT tag unless already marked from a past capture. We then compared a transmitter to the body width of each snake to determine which transmitter would be suitable. Only snakes wide enough for the smallest transmitter and over 220g would be considered. We examined each snake to ensure good health; this included checking the body condition (for example if the snake was emaciated), and presence

of disease or injury. If suitable for surgery, the individual was securely transported in a dark cloth bag inside a ventilated plastic container back to the lab at Bangor University.

Surgeries were completed by a qualified person and anaesthesiologist following the surgical implantation methodology Reinert and Cundall (1982). The surgery was a short process involving sedating the snake and inserting the radio transmitter inside the coelomic cavity. The transmitter size was constrained by the diameter of the body cavity, due to the requirement to allow gut content to pass. We used Holohil BD-2T transmitters (Holohil Inc, Carp, Canada) and selected two different-sized transmitters 1.2g and 1.6g. Most snakes were given the large transmitters because they have the longest battery life (10-20 weeks, average 14 weeks). This would help to ensure the transmitters would last the full tracking period. However, one snake was given a smaller transmitter due to its size. Many of the snakes captured were too small for either transmitter size and because of the difficulty finding adults, we had to use any snake that could tolerate a transmitter. Each snake had a radio transmitter with a unique frequency, this was checked several times to ensure it was functional and the frequency matched our records. Snakes were held for several days after their capture (2.286 ± 0.951 ; range 1-4 days) until a qualified person could complete the surgery. Their recovery was monitored post-surgery until the snakes regained consciousness and examined before release to ensure the surgical wound was not bleeding and the stitching was in place. Snakes were released the following day after surgery at the site of capture or as close as possible, in temperatures over 14°C. Radiotracking started the following day, as previous radiotelemetry studies on snakes found movement and behaviour appeared to return to normal the day after release (Hodges *et al.*, 2022; Smith *et al.*, 2021). Therefore, all telemetry data was included in our analysis from the first tracking day.

Radiotelemetry procedures

The tracking period was from May to August when the snakes were active.

Reproductive cycles and environmental constraints result in snakes having a small activity window with peaks in movement between May and July. From August to September snakes are still active but after breeding and oviposition, there is less need for them to move as their reproductive period has ended. The study duration covered most of their active time finishing just before hibernation in October, but the movement had already significantly slowed down towards the end of August.

Following the guidelines in our home office licence the transmitters were left inside the snakes after the study ended. Each was tracked five times daily in regular two-hour intervals (09:00, 11:00, 13:00, 15:00, 17:00) or as close to these intervals as possible depending on the time taken to locate individuals. High frequency tracking data is essential to catch animal movements and discern behaviour beyond shelter site use. Only five snakes were tracked at any time; tracking started before the first interval to ensure fixes were as close to 09:00. Snakes were tracked in the most efficient order to get fixes recorded as close to the set intervals.

As a diurnal species, this schedule enabled us to start before the daily movement began and after the movement had stopped on most days. We used VHF telemetry equipment, comprising of a VHF yagi antenna (Perdix) and TRX-48S receiver (Wildlife Materials), to locate the signal. The location of the snake was confirmed either visually or by precisely triangulating a three-point to estimate within a 5m radius. Triangulation allowed greater accuracy when determining positions inside buildings, underground refugia, dense vegetation, or zoo enclosures. When possible, we kept a distance of $\geq 10\text{m}$ to minimize disturbance. Once the location was confirmed the observation date (dd/mm/yyyy), time (hh:mm), coordinates (UTM, WGS-84), GPS accuracy (m), whether the snake had relocated, and any notable observations were all recorded. Surgeries and radiotelemetry procedures for this study were followed in accordance with the Animals (Scientific Procedures) Act 1986 and Bangor University Animal and Welfare Ethics Review Board and the Home Office project license PC44793B6 (license holder John Mulley).

QGIS habitat feature shapefile

We first had to create our own habitat feature shapefile map (see Figure 2) that would serve as the base of the statistical analyses. This was achieved using QGIS Desktop ver. 3.26.2. Satellite imagery and in-person confirmation was used to create new polygons which were drawn over selected habitat features as new vector layers which would be our variables. These features were roads, bare ground, hedgerows, meadows, pastures, woodland, gardens, buildings, and scrub. We later combined bare ground and roads to create road surfaces, this gave us a total of eight habitat features.

Meadow was defined as being mostly natural fields and untended to by people with a sward height of over 20 cm, whereas pastures are fields that are maintained by gardening, mowing, or strimming with a sward height below 20 cm. We selected roads because they are known barriers for wildlife and the study site is surrounded by busy main roads. We predict that *Z. longissimus* will choose hedgerows when moving, this feature separates and encloses most of the fields and roads. Woodland, scrub, buildings, and bare ground features were present in the study area so were also included. Scrub was defined as gorse or short woody vegetation that is not actively maintained, and bare ground is best described as a concreted area such as a car park. Zoo grounds and residential gardens were categorised as gardens due to their generally high disturbance and similar structure. We then used the field calculator in the attribute table to calculate the area and perimeter of each feature. Finally, we merged all vector layers and saved this as a shape file, which was exported into R studio for analysis. All analyses were completed in R v4.2.0 using RStudio 2022.07.1+554 (R Core Team, 2022; R Studio Team, 2020).

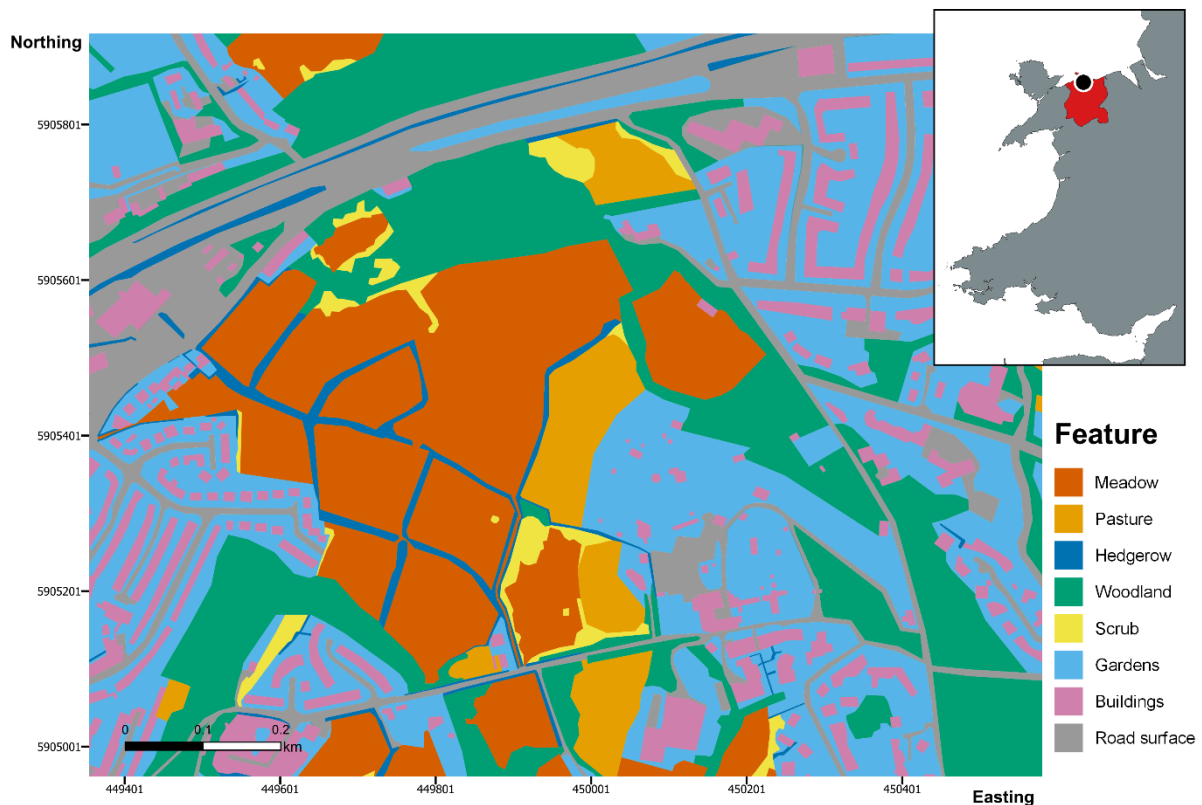


Figure 2. Study site map illustrating the habitat features covering the study site. The inset map of Wales illustrates the study site location shown by the black marker in Conwy borough county highlighted red in Wales. Habitat feature and Wales map both created in QGIS v.3.26.2 (<https://qgis.org/>).

Integrated step-selection functions

We used a Resource Selection Function called Integrated step-selection functions (ISSF) that compares recorded locations (used) to available locations using very high frequency (VHF) radiotelemetry data. This analysis can compare Euclidean distance to habitat features against the available locations determined by the previous location using logistic regression to identify habitat association or avoidance. The comparison between used and available habitat features using steps allows movement and habitat selection to be modelled together to define habitat availability relating to movement constraints (Forester *et al.*, 2009; Avgar *et al.*, 2014; Thurjfell *et al.*, 2014; Fieberg *et al.*, 2021). Unlike other resource (habitat) selection analyses, ISSF links consecutive locations (steps) together. Thus, it can provide estimations of

the relationship between habitat selection and movement which help to predict movement patterns and identify fine-scale behavioural interactions between an animal and its environment (Fieberg *et al.*, 2021).

This method creates a set number of randomly generated locations or steps from movement variables which include the step length (distance between locations) and turning angles (direction) (Thurjfell *et al.*, 2014). To estimate movement and habitat variables we can use the following steps: 1) estimate movement parameters from the recorded step lengths and turn angles from our data, 2) randomly generated steps are created from the previous location which is used to generate time-dependent availability distributions, 3) randomly generated steps are combined with the time-dependent to estimate habitat selection parameters using conditional logistic regression (Fieberg *et al.*, 2021). Using these parameters combined with movement characteristics (both step length and turning angles) can improve estimations during the first step to reduce bias of habitat selection in the analysis (Avgar *et al.*, 2016). We included the data from six of the individuals, we excluded M074 from the analysis due to its stationary behaviour. It remained in the same refugia for most of its tracking duration (n=29 days). For individual selection, we created ISSFs using amt package v.0.1.7 (Signer *et al.*, 2019) using a modified script from Smith *et al.* (2021).

We imported the habitat feature shape file into RStudio and created raster layers for each feature. Raster layers included continuous values by calculating the distance between two points (Euclidean distances) from individual raster cells to habitat features (Smith *et al.*, 2021). Zero inflation is caused by more zeros being present in the data than expected when modelling count variables and can lead to invalid inference if ignored. Therefore, our raster layers were inverted to prevent zero-inflation of distance to habitat feature values. Inverting a raster layer switches the cell values so negative values will demonstrate an avoidance. This aided in the identification of habitat feature selection and interpretation of model outputs for example, a negative effect will be classed as avoidance (Marshall *et al.*, 2020; Smith *et al.*, 2021; Hodges *et al.*, 2022). We created nine single-factor models which included step characteristics (length and turning angles) as covariates, with model 1

(null model) only including step characteristics, and the other eight models using one single feature.

Step length was created from a gamma distribution and turning angles from a von Mises distribution and was generated from the recorded locations (Avgar *et al.*, 2016; Signer *et al.*, 2019; Smith *et al.*, 2021). Both step length and turning angles were included to reduce bias and more accurately indicate the choice of habitat selection (Thurjfell *et al.*, 2014). We extracted the covariates from the endpoint of the step and created two hundred random steps for each used location because of the smaller dataset and the computational power needed for this analysis. The same starting point was used for both recorded and random steps. When creating the tracking data, we used a resampling rate every two hours with a tolerance of four hours. Akaike's Information Criteria (AIC) determined the performance of the models, with the top-performing models having a lower AIC value, indicating that a model is more supported by the data than a model with a higher AIC value.

We continued to include selection at a population level by including all the data from each individual, once again we used a modified script from Smith *et al.*, 2021 originally adapted from Muff *et al.*, 2019. We used a mixed conditional Poisson regression model with the step and individual being modelled as Gaussian processes (Hodges *et al.*, 2022). A similar process to the individual ISSF was used, by creating nine single-factor models from the inverted rasters of habitat features including random intercepts and slopes. We again resampled the tracking data (two hours with a tolerance of four hours) and generated two hundred steps including step length and turning angles. For the models, we ran an integrated nested Laplace approximation model (INLA package v.22.12.16; Rue *et al.*, 2009) which can be used for Bayesian analyses. It is also useful because of its speed and ability to compare models under different criteria and for predictive Bayesian inference (Rue *et al.*, 2009). Following Smith *et al.* (2021) the step (random effect) had a fixed prior precision of 0.0001 and for the individual (random slopes) we set the Penalized Complexity prior to 1, 0.05 and uninformative normal priors, Normal to 0, 103 for fixed effects. The R code for all analyses has been provided (see Supplementary material 1).

Results

Capture summary

A total of seven adult male *Z. longissimus* were captured and implanted with radio transmitters for the study (see Table 1). The capture usually was mostly opportunistic (n = 5), but also included snakes caught during a dedicated survey (n = 1) and captured by a member of the Welsh Mountain Zoo staff (n=1) (Appendix Table 1). Snakes of a suitable size were infrequently found during surveys, with juvenile snakes being more common. Larger snakes were often found opportunistically during or between the tracking of other snakes. We recorded one mortality during the study. M031 was run over by a vehicle. The snake was recorded close to a road and blood was also found on the road close to its location, and a dissection confirmed the injuries were associated with vehicular trauma (n = 1).

Table 1. Morphometric data summary including the fate of all radio-tracked Aesculapian snakes (*Zamenis longissimus*) in Colwyn Bay, North Wales over the 2022 season (May-August). Including the ID, biometric measurements, transmitter size used and fate of each snake.

Snake ID	Sex	SVL (mm)	Mass (g)	Transmitter size	Fate
M031	Male	960	383	Large (1.6g)	Dead, run over by a vehicle.
M074	Male	1089	399	Large (1.6g)	The transmitter battery died, confirmed by snake recapture
M154	Male	971	398	Large (1.6g)	Survived
M202	Male	1200	498	Large (1.6g)	Survived
M209	Male	982	475	Large (1.6g)	Survived
M217	Male	801	235	Small (1.4g)	Unknown, Transmitter signal lost
M218	Male	1115	522	Large (1.6g)	Survived

Movement summaries

Snakes were tracked for a mean of 53.57 ± 28.94 days (range = 17-101 days), resulting in 1767 total fixes (252.43 ± 133.6 ; range = 83 – 457 observations) and 368 total relocations (range = 6-155 relocations) between 12-05-2022 to 20-08-2022 (see Table 2; Figure 3). Individuals were located on average every 5.04 ± 0.16 h between fixes (range = 0.35 – 93h; Figure 4). During their tracking durations the total distance the snakes moved averaged $3274.14\text{m} \pm 2574.76$ (individual total distance moved range = 585-7125m). Edgar and Bird (2006) stated male *Z. longissimus* can travel up to 2000 m during the breeding period (total duration was not mentioned) to locate female snakes. We found the maximum distance moved in one relocation ranged between 129.11-689.38m ($440.98 \pm 214.04\text{m}$). Snakes had a mean daily displacement (MDD) of $55.54 \pm 24.54\text{m}$ (range= 19.4-91.6m).

Table 2. Tracking summary including dates, number of days and fixes, and distances moved for each Aesculapian snake (*Zamenis longissimus*) in Colwyn Bay, North Wales between May and August 2022.

Snake ID	Start date	End date	Days tracked	Total number of fixes	Number of relocations	Total distance (m)	Mean daily displacement (MDD)	Maximum distance (m)
M031	08/06 /2022	11/07 /2022	34	165	43	1107	33.3	129.11
M074	16/07 /2022	15/08 /2022	31	145	6	585	19.4	423.29
M154	18/06 /2022	20/08 /2022	64	302	73	2734	43.2	468.88
M202	12/05 /2022	20/08 /2022	101	457	155	6846	68.3	632.88
M209	26/05 /2022	20/08 /2022	87	423	131	7175	83.2	689.38
M217	15/06 /2022	01/07 /2022	16	83	32	812	49.8	132.69
M218	11/07 /2022	20/08 /2022	41	192	54	3660	91.6	610.59

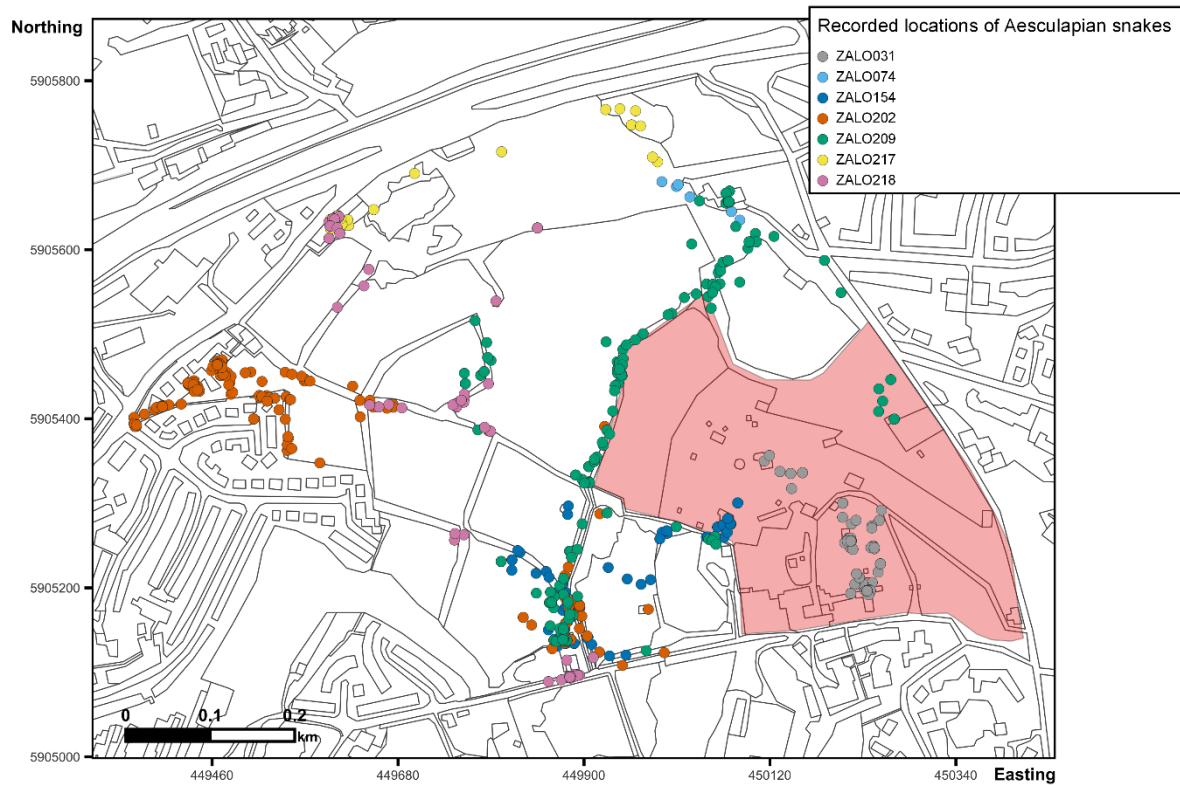


Figure 3. Map of the study area in Colwyn Bay, North Wales with all recorded locations of each telemetered Aesculapian snake (*Zamenis longissimus*) during the study period in 2022. The highlighted section in red is the Welsh Mountain Zoo, from where the snakes originally escaped.

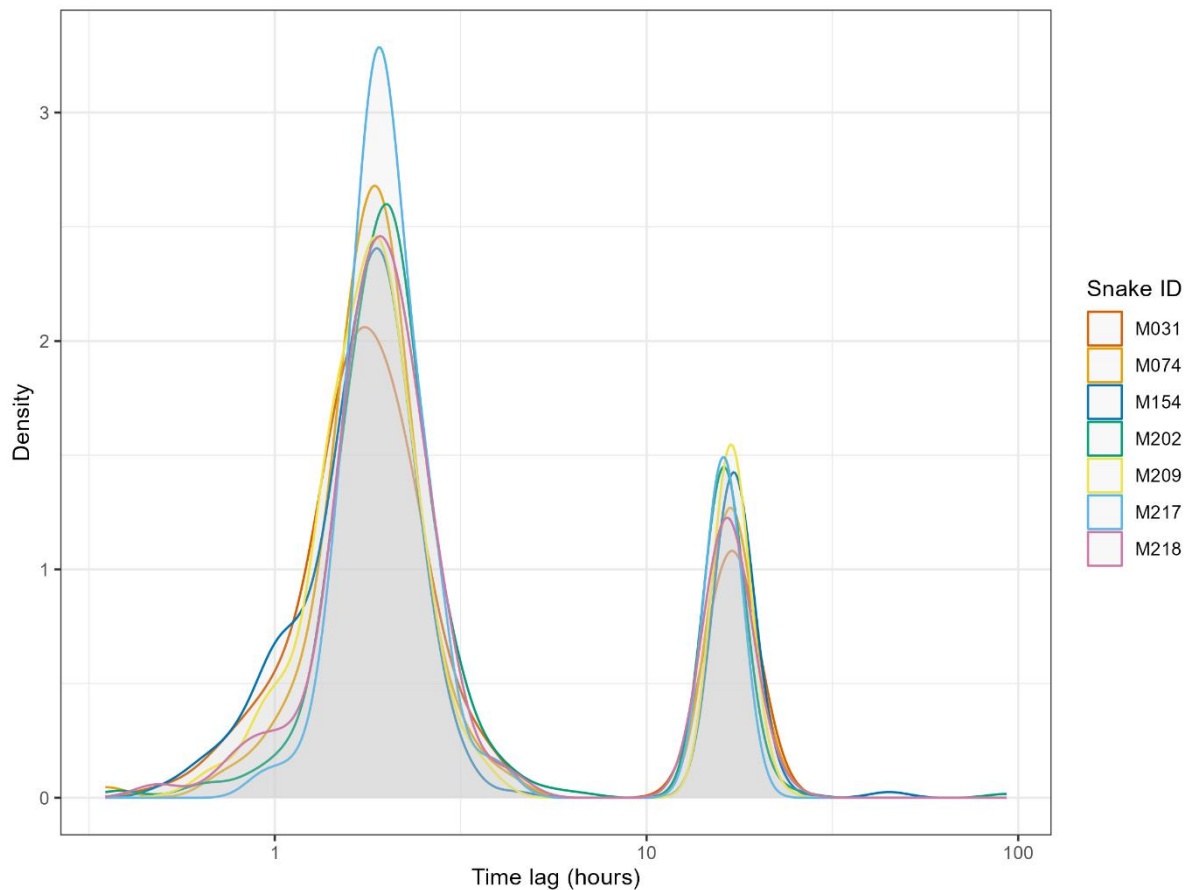


Figure 4. A density plot of the time lag (in hours) between recorded fixes for all Aesculapian snakes (*Zamenis longissimus*). The gap between the two peaks indicates the time overnight without fixes.

Not all individuals were tracked for the full duration of the study period due to early transmitter failures ($n = 2$). The signal of M217 was lost after only sixteen days and the cause for this is unknown. Possible reasons could have been mortality, transmitter failure or damage, or the individual moving outside of the signal range despite a wide search area and effort. The most likely reason was due to its smaller-sized transmitter, which we suspect ran out of battery more quickly than expected. The transmitter used for M074 also ran out of battery before the end of the study period, confirmed by the recapture of the individual. Although we aimed to track each individual five times each day, occasionally we were unable to locate snakes for consecutive fixes or days (see Figure 5). There were small gaps in the tracking data where some observations were missed due to snakes traveling long distances and being difficult to locate, or being located underneath structures that gave off a weak

signal. In the case of M154, we missed observations (n = 1 day) due to a weak signal towards a zoo enclosure with a large pool of water. We suspected the snake was situated underneath the concrete because of the signal direction. The snake was seen emerging out of a hole inside the enclosure the next day. We were also unable to record the location of M202 for several days (n=3). Again, we suspected the transmitter battery to have run out because of difficulty triangulating the signal. A random signal was found accidentally on another frequency which was confirmed to be M202 by capturing the snake. The reason for the transmitter changing frequency is unknown but was still functional and we were able to continue radio tracking the individual on the new frequency until the end of the study.

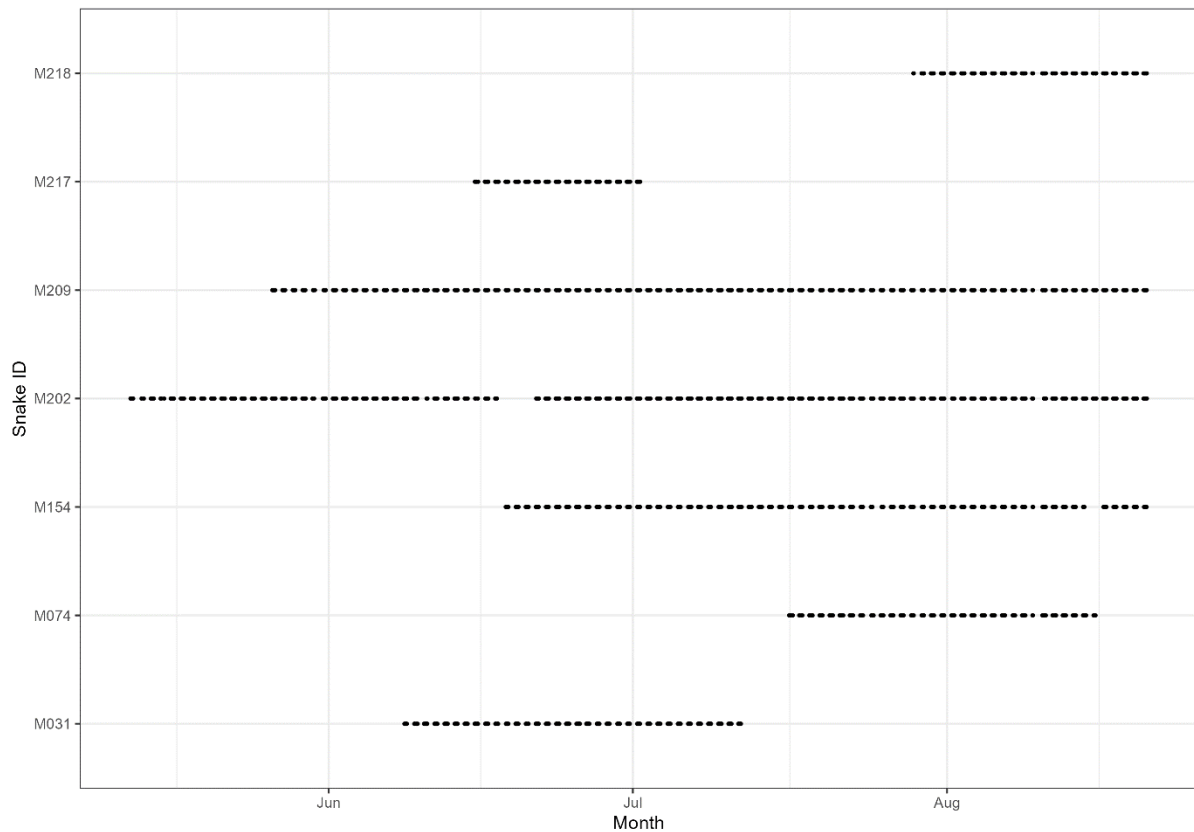


Figure 5. Illustration showing the tracking durations of all Aesculapian snakes (*Zamenis longissimus*). Vertical lines represent the overlap of simultaneously tracked individuals and consistency of tracking for each snake from the first to the final tracking date, breaks in the line indicate a gap in tracking.

Integrated step selection analysis

Four of the models from the individual ISSF models and AIC scores best described the habitat selection of Aesculapian snake individual movements (see Table 3). The top models for predicting the movements for individual snakes included model 3 (pasture), model 4 (hedgerow), model 7 (gardens), and model 8 (buildings). Both model 4 and model 8 performed best for two individuals, with model 4 performing best for M154 and M29 and model 8 performing best for M031 and M202. Model 3 performed best for one individual M218 and model 7 performed best for M217. Distance to feature indicates if a snake selected to move towards a habitat feature, positive estimations indicate the selection of a habitat feature because of our inverted raster layers.

Table 3. Individual model formulas including the AIC scores from individual Integrated step select function models. The bold text illustrates the Akaike's Information Criteria scores within $< 2 \Delta$ AIC for top models from the recorded locations for each snake. Each model (except for the null model) contains a habitat feature, step length, and turning angle. Abbreviations for sl: step length, ta: turning angle.

Model	Model formula	M031	M154	M202	M209	M217	M218
model1	log_sl*cos_ta + strata(step_id_) (null model)	259.24	511.02	1043.6	824.22	163.58	281.12
model2	Meadow + Meadow:sl + Meadow:ta	264.19	513.98	1027.25	822.31	168.97	283.61
model3	Pasture + Pasture:sl + Pasture:ta	264.63	510.81	1045.25	825.61	166.63	275.48
model4	Hedgerow + Hedgerow:sl + Hedgerow:ta	264.98	500.18	1040.63	817.82	163.32	280.43
model5	Woodland+ Woodland:sl + Woodland:ta	264.64	514.33	1037.56	829.7	165.05	285.73
model6	Scrub + Scrub:sl + Scrub:ta	264.95	504.34	1041.77	827.66	165.56	283.6
model7	Gardens + Gardens:sl + Gardens:ta	256.58	501.33	1034.5	829.84	161.07	281.57
model8	Buildings + Buildings:sl + Buildings:ta	251.97	500.65	1019.97	829.16	165.4	282.03
model9	Gardens + Gardens:sl + Gardens:ta	262.27	510.04	1042.36	830.19	163.5	282.62

Of the six *Z. longissimus* included our individual analysis, three exhibited a positive association and two individuals exhibited an avoidance of habitat features (Figure 6). We could infer two snakes had a positive association with meadows with one further possible association, pasture was selected by two snakes with one further possible association. We identified possible associations when the estimate was greater than zero for example a positive effect (≥ 2) and overlapping intervals that approached zero (Appendix Table 2). Gardens were another feature selected by two snakes and one other potentially associated. We determined that M218 was positively associated with scrub and hedgerows. We determined the avoidance of roads in M202 and pasture in M031. Broad confidence intervals were visible for multiple individuals as we were unable to determine any preference. When the confidence intervals for a feature overlap zero it indicates a feature can't be described as having any association possibly due to model uncertainty.

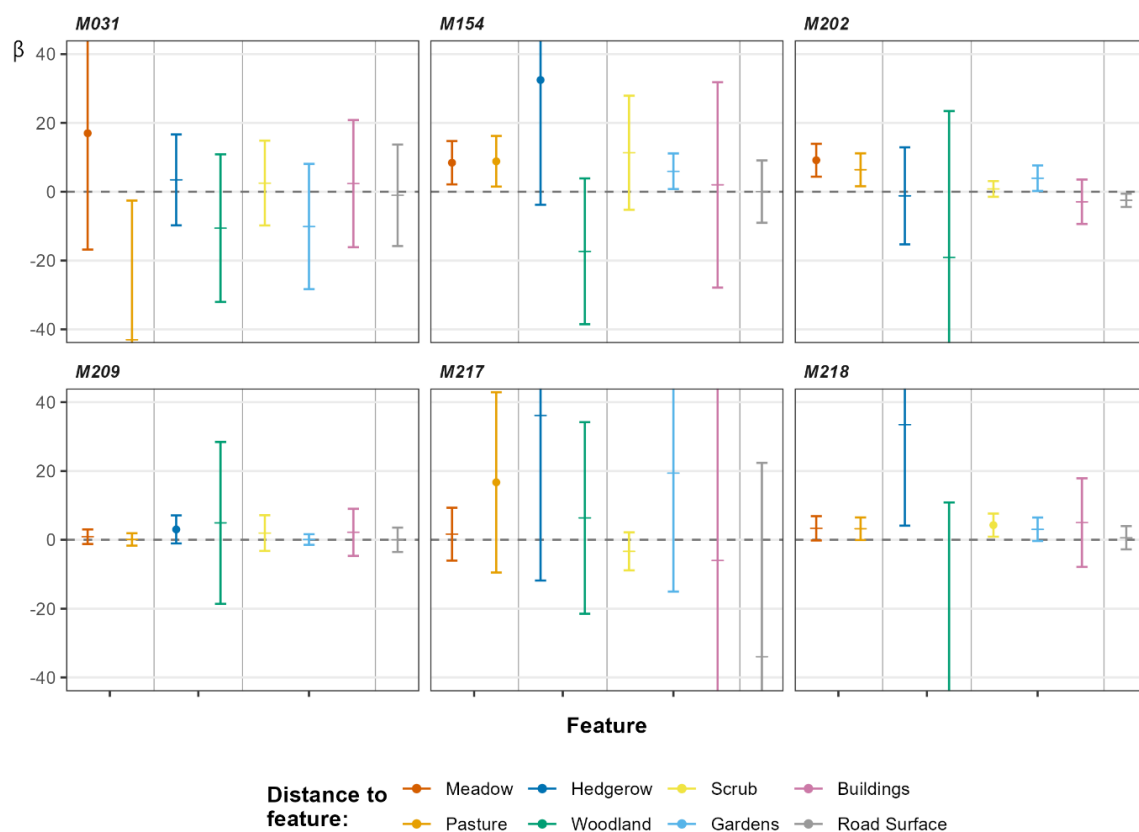


Figure 6. Integrated step selection functions for distance to habitat features for individual Aesculapian snakes (*Zamenis longissimus*). Positive values indicate a preference towards a habitat feature. Error bars show 95% confidence intervals.

This model uncertainty could be caused by our small data set combined with long periods of inactivity from the snakes. For M217 who was tracked for only seventeen days before the transmitter signal was lost, model uncertainty was probably caused by a lack of recorded fixes.

Individual-level analysis of step characteristics with habitat features indicated that shorter step lengths were taken when closer to buildings in M202, and pasture and hedgerows in M218. Other features that approached significance included longer distances taken towards scrub and woodland in M202 and gardens in M031, shorter distances approaching significance were roads for M154, buildings in M218, roads and gardens in both M202 and M218. No associations were present in the other individuals with all confidence intervals overlapping zero (Figure 7).

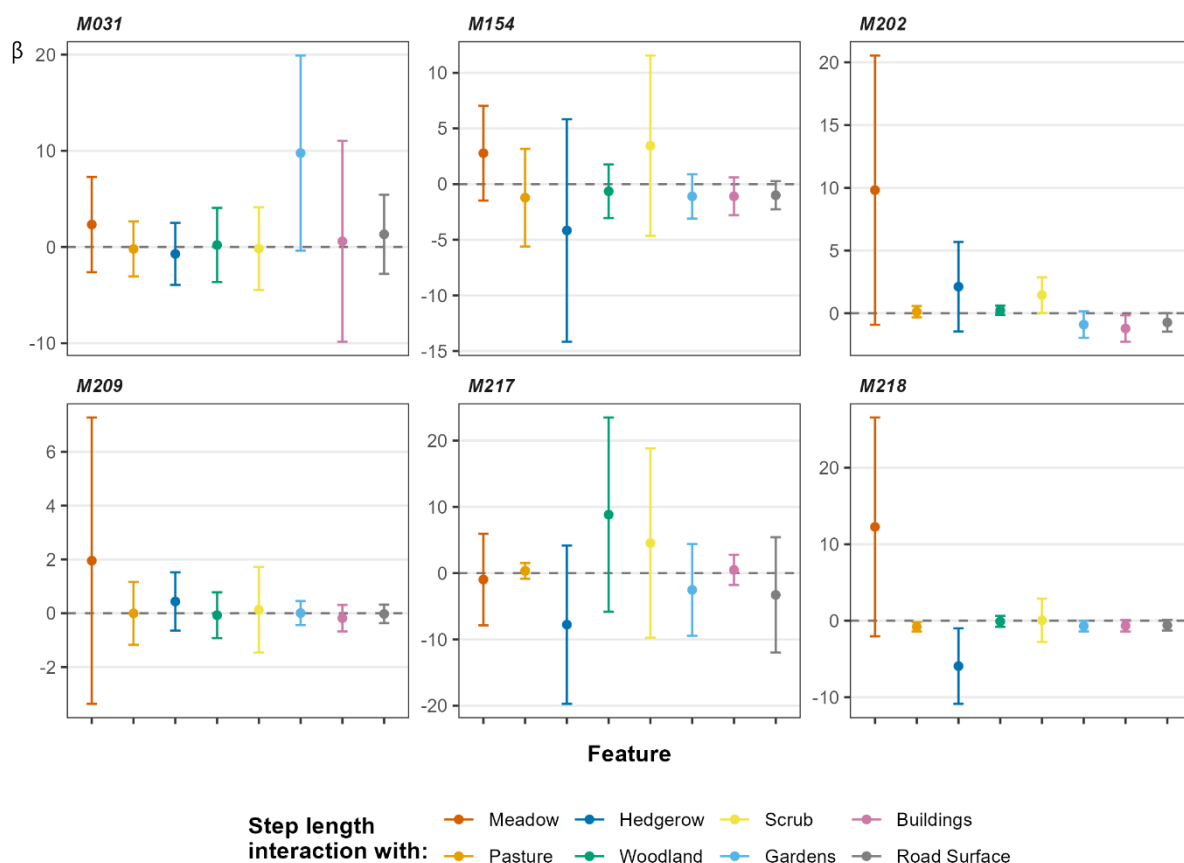


Figure 7. Integrated step selection functions for each of the tracked individuals showing interactions between step length and habitat features for Aesculapian snakes (*Zamenis longissimus*). Error bars show 95% confidence intervals.

Using a population-level model absorbed some of the individual variation to highlight larger trends. At a population level, *Z. longissimus* had a positive association with hedgerows (mean estimate = 0.211, 95% confidence intervals 0.0095-0.0409), scrub (mean estimate = 0.0083, 95% confidence intervals 0.0003-0.0172), and buildings (mean estimate = 0.0255, 95% confidence intervals 0.0015-0.0535; Figure 8; Appendix table 3). A possible weak avoidance of woodland was present, but this could not be determined with certainty. We found no statistically significant avoidance of any of the features. There was no clear relationship between step length and any feature, all features had overlapping confidence intervals (Figure 8). This suggests at a population level step length was either unable to predict movement due to model uncertainty or step length was of little importance when selecting habitat features despite clear individual preferences. Although we could not definitively determine step lengths with any feature, it could be suggested snakes used longer step lengths when closer to hedgerows and woodland as these features approach significance.

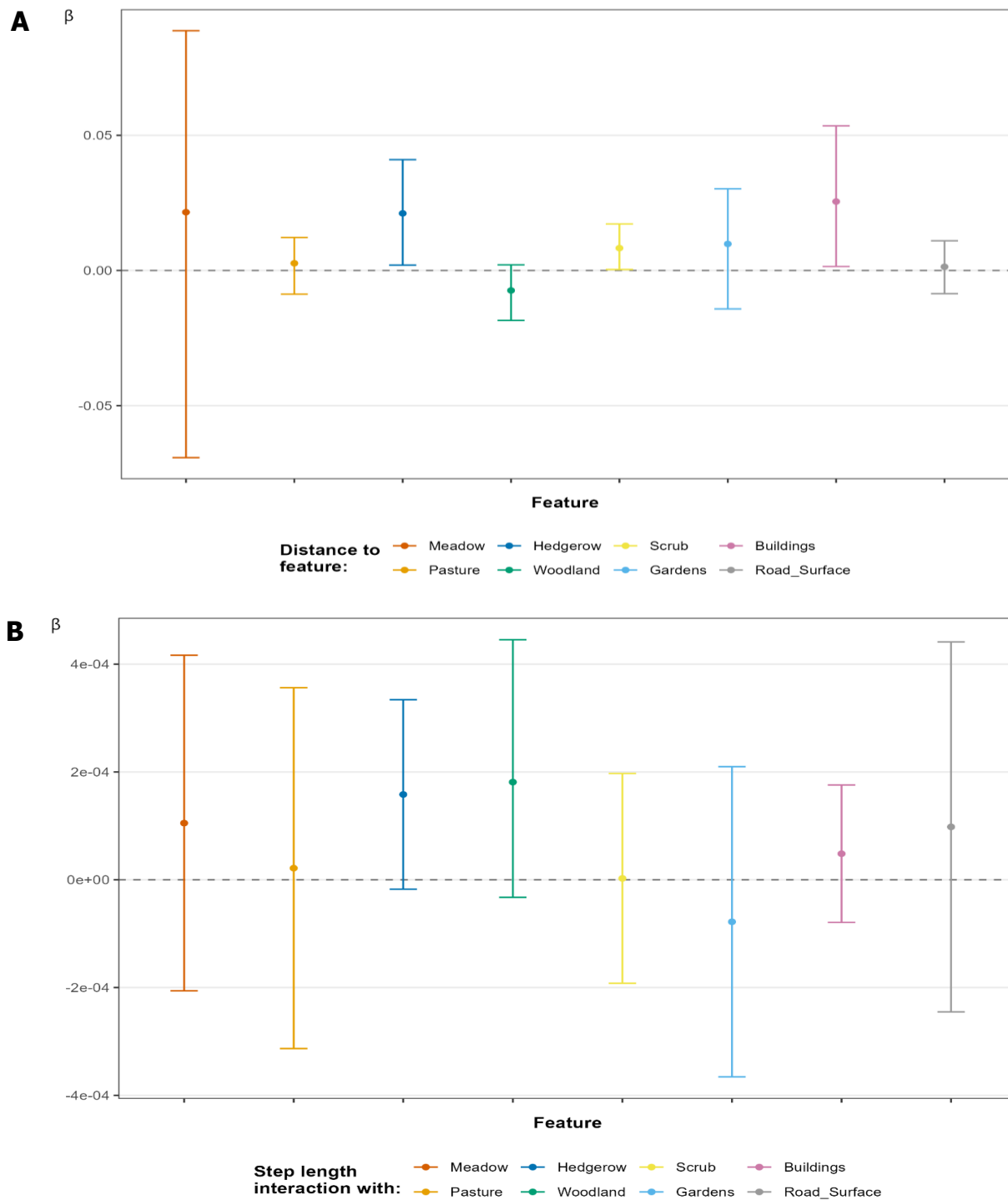


Figure 8. A) Distance to habitat features at a population level for all male Aesculapian snakes (*Zamenis longissimus*) excluding M074. Positive values indicate a selection towards a habitat feature. B) Step length interaction with habitat features at a population level for all male Aesculapian snakes (*Zamenis longissimus*) excluding M074. Error bars for both graphs show 95% confidence intervals.

Discussion

The main findings from our analysis revealed differences between individual and population habitat preferences during movement, that indicates high levels of heterogeneity. The population level analysis showed snakes selected areas closer to hedgerows, scrub, and buildings, which reflected our observations during tracking. Snakes were frequently recorded using these features when travelling between sheltering locations. Individuals exhibited varied preferences; meadows, pastures and gardens were selected by two individuals, and one snake selected both scrub and hedgerows. Road avoidance was found in one snake and pasture in another. We found habitat features influenced step length in our individual analysis but not the population level analysis. Individuals had shorter step length interactions with hedgerows, buildings, and pastures.

This research is among the first to use radiotelemetry and advanced analyses to investigate habitat selection and movement of the introduced population of *Z. longissimus* in the UK. Furthermore, previous literature on the habitat preferences of this species in its native range have not used advanced analyses to investigate its movement ecology. Our study is also one of few movement ecology studies on any snake species to include movement when examining habitat selection. This study aimed to track adult male *Z. longissimus* in Colwyn Bay, North Wales to identify habitat selection during movement to establish known pathways and predict dispersal routes or barriers. We also wanted to determine the relationship between the location of *Z. longissimus* when moving to their distance from a habitat feature during their active period between April and September.

Despite advancements in methodology for data collection and analyses, reptile spatial ecology studies over the last twenty years have shown little progression (Crane *et al.*, 2021; Mercker *et al.*, 2021). Habitat selection continues to be analysed as presence or absence data rather than simultaneously modelling selection and movement (Beyer *et al.*, 2010). Habitat availability is usually considered constant through time therefore all habitat is equally available to the animal at any time within a determined area (Fieberg *et al.*, 2021; Kunegel-Lion *et al.*, 2022). Step selection functions relax this assumption by calculating availability from the previous

location and movement characteristics (Thurjfell *et al.*, 2014). This allows for habitat availability to have time-specific parameters and, therefore considers animal movement when determining habitat selection (Fieberg *et al.*, 2021). Habitat selection analyses that incorporate movement are routinely used in studies of large mammals but are seldom done in reptiles (Northrup *et al.*, 2022).

Analyses such as ISSa (Integrated Step Selection analyses) can help achieve a better understanding of reptile movement and should be included more frequently in future studies. Our study demonstrates the practicality of using advanced habitat selection modelling, which can be applied to coarser data sets and resolve common issues when studying snake movement, including infrequent movement periods (Crane *et al.*, 2021; Northrup *et al.*, 2022). Using ISSa allowed the use of all fixes, including short moves, which can inform larger decisions as to why and how a snake chooses to move (Maag *et al.*, 2022). Our tracking frequency enabled us to capture smaller movements throughout the day before returning to the previous location. Less sensitive tracking sampling could miss smaller movement patterns which also influence selection. We were also able to model both population and individual preferences as individual variation is an important consideration in any habitat selection study (Northrup *et al.*, 2022). At the population level, we found no significant results for step characteristic (length and turning angle) interactions, although preferences were found in some individuals. Our inability to draw conclusions from the population results may be due to our small sample size and individual heterogeneity. Studying a species or population is useful for answering broader questions on movement but ultimately fails to consider individual heterogeneity (Feuka *et al.*, 2022). A study on invasive brown tree snakes in Guam by Feuka *et al.* (2022) also found high levels of individual heterogeneity in their movement patterns, this variability weakened their inference of their population analysis results.

The results from population level analyses may not represent individual preferences. Invasive species management and eradication is dependent on the detectability and removal success of individuals from a population. Individual snakes may have a higher catchability due to their habitat preferences and movement patterns (Whiting,

Dixon and Nelson, 1996). Not accounting for individual heterogeneity could cause inaccurate assessments, and likely limit the effectiveness of targeting specific environmental features (Vindenes and Langangen, 2015; Hamel, Gaillard and Yoccoz, 2018). Despite this, individual heterogeneity is often not considered when studying snake populations; even though it is well-documented among reptiles (Vindenes and Langangen, 2015). This is important considering the non-native status of *Z. longissimus*, as few individuals can dictate the speed and success of establishment and range expansion.

Habitat selection in Aesculapian snakes has been comprehensively studied in their native range where the species is known to occupy a wide range of habitats (Capula and Luiselli, 2002; Rugiero and Luiselli, 2004). Both native and introduced North Wales populations exhibited preferences for multiple habitat features (Rugiero *et al.*, 2020). Generalist species with less restrictive habitat requirements have higher survivability and success in urban environments compared to specialist or terrestrial species with lower mobility (Breininger *et al.*, 2011). As a highly mobile species capable of arboreality, *Z. longissimus* has fewer constraints for dispersal increasing its ability to move between fragmented habitats (Breininger *et al.*, 2011). Snakes climbed several meters to access trees, buildings, and dense vegetation. Hedgerows act as pathways between refuge sites and provide both arboreal and terrestrial microhabitats that connect multiple habitat features offering opportunities for thermoregulation, shelter, and prey (Pulsford *et al.*, 2017; Guiller *et al.*, 2022). We observed mosaic basking either on top of hedgerows with small sections of their bodies visible or fully exposed on branches. Certain hedgerows were used regularly by multiple individuals, four snakes were repeatedly found along two specific hedgerows. Snakes at their thermoregulatory limit may select pathways that provide the best conditions for their thermal and energy requirements at the same time providing suitable cover (Harvey and Larson, 2020).

Our observations and population selection of buildings were consistent with previous studies of native populations where anthropogenic features are highly favoured (Kovar *et al.*, 2016a; Kurek *et al.*, 2017; Kurek *et al.*, 2018; Lelievre *et al.*, 2010). In Northern populations where environmental conditions are suboptimal, snakes are

heavily dependent on anthropogenic features (Kovar *et al.*, 2016a). Most individuals from the North Wales population exhibited site fidelity, frequently returning to the same sheltering locations. We located four snakes frequently sheltering in the same building and multiple snakes in the attic simultaneously. Moulded skin was discovered on drainpipes and inside attic spaces of sheltering locations indicating snakes used buildings for ecdysis. Anthropogenic structures provide multiple benefits including shelter from potential predators or human-related threats, creating safer pathways in otherwise open or highly disturbed areas (Yu *et al.*, 2022). In North Wales, buildings may provide a more suitable microclimate than other available features.

Previous habitat selection studies in their core range by Ioannidis and Bousbouras (1997) and Kovar *et al.* (2016a) found snakes were positively associated with dense woody vegetation or scrub. Scrub may provide safety when moving through open fields which were often hunting grounds for birds of prey, particularly buzzards (*Buteo buteo*). We found limited evidence supporting this preference as it was selected at a population level and in one individual for distance to feature only. Where our results differed from previous studies was toward woodland preferences, in warmer climates available in southern Europe snakes are located within deciduous woodland (Musilová *et al.*, 2010; Rugiero *et al.*, 2002; Ioannidis and Bousbouras, 1997). We found no evidence supporting woodland preferences, similar to northern isolated populations in the Czech Republic and Poland (Kovar *et al.*, 2016a; Kurek *et al.*, 2017; Kurek *et al.*, 2018).

As a non-native species in the UK, it is crucial we continuously monitor populations of *Z. longissimus* to inform mitigation plans and establish its invasive potential. The success of controlling introduced snake populations is highly dependent on the available data on the target species (Maestresalas *et al.*, 2023). Knowledge of spatial ecology can positively contribute to their management and the implementation of more effective control methods (Maestresalas *et al.*, 2023). Snakes are often more abundant than results suggest from visual surveys as surveyors may fail to detect individuals in dense vegetation, burrows or buildings (Matthias *et al.*, 2021). Engeman *et al.* (2018) focused surveys on fences used by *B. irregularis* as movement pathways and found that targeted searches consistently produced

captures at low levels. Searching known pathways may increase detectability, but *Z. longissimus* are difficult to locate even when using radiotelemetry (Capula and Luiselli, 2002; Boback *et al.*, 2020). During surveys, a proportion of individuals using inaccessible features for example dense vegetation, burrows, or anthropogenic features will be missed (Boback *et al.*, 2020; Guzy *et al.*, 2023; Maestresalas *et al.*, 2023).

Identification of environmental features for targeted visual surveys and trap placement can reduce effort and maximise capture success (Veitch *et al.*, 2019). A weak understanding of interactions between trap design and placement in an environment can impact eradication prospects (Batoszek *et al.*, 2021). Trap positioning can influence capture probabilities and should be placed where snakes are most likely to be encountered. As an example, for *B. irregularis* trapping was most successful when placed in preferred areas along forest edges but trap efficacy decreased over time (Engeman *et al.*, 2018; Nafus *et al.*, 2021). Trapping could be used to eliminate sexually mature adults and must be continual to catch newly matured snakes (Febrer-Serra *et al.*, 2023). Using traps can be labour-intensive and resource consuming so focusing on specific locations is essential in designing effective strategies. A combination of both targeted searching and trapping results in greater removal effort and results (Goetz *et al.*, 2021). This research has provided a foundation that forthcoming ecological studies can continue to build to understand how this species continues to persist and considerations about their future.

Limitations

I acknowledge the limitations in this study, following the guidelines of the STRANGE framework to identify, mitigate, and declare sampling biases to improve replication in research with animals (Webster and Rutz, 2020; Rutz and Webster, 2021). We recognise one key limitation is trappability and self-selection from the STRANGE framework (Webster and Rutz, 2020; Rutz and Webster, 2021). There was a possibility *Z. longissimus* were more likely to prefer anthropogenic features because snakes were captured close to features such as buildings, gardens, or the enclosures

inside Welsh Mountain Zoo. A problematic factor in the reproducibility of our study was the potential behavioural differences between individuals. A non-random sample caused by individual preferences may increase the chance of capture, influencing our understanding of the population as a whole. One example would be a hedgerow frequented by multiple snakes at a certain property. We were able to catch multiple snakes basking on this hedgerow over the study. With our frequent sampling schedule, it was also possible our tracking could have influenced snake behaviour or movement patterns despite attempts to limit disturbance. Sex-biased dispersal was one reason only male snakes were selected, however, differences between the sexes could also limit the effectiveness of our recommendations. Targeting female snakes is more important in reducing the population size; females are likely the limiting sex for population growth (Febrer-Serra *et al.*, 2023).

Recommendations for future studies

Future research should focus on tracking the Welsh population of snakes over multiple years with the inclusion of female snakes providing a comprehensive look at habitat selection. In addition, the habitat preferences of juveniles can vary compared to adults and the dispersal capabilities of juveniles are unknown. It is crucial we understand their dispersal capabilities and population dynamics over their complete lifespan to identify the impacts this species could have in North Wales.

The future impacts of global climate change will be significant (Hoegh-Guldberg *et al.*, 2019). Forecasted warmer temperatures can contribute to increased introductions, establishment, dispersal, and environmental impacts of invasive species (Hulme, 2016; Vilizzi *et al.*, 2021; Borden and Flory, 2021). Future climate conditions may allow for range expansions northward especially for species with broader distributions and thermal tolerances (Walther *et al.*, 2009; Vilizzi *et al.*, 2021). Global warming has aided invasive species to spread to previously unsuitable environments where survivability was low and reproduction unsuccessful (Walther *et al.*, 2009). For *Z. longissimus* in North Wales, increased temperatures could reduce thermal constraints and reliance on anthropogenic features also increasing

abundance and dispersal rates. Milder temperatures during the winter could remove constraints affecting the duration of time snakes are active possibly increasing reproductive rates and development of offspring. Therefore *Z. longissimus* should continue to be monitored and research into how current and future temperatures may affect the viability and success in the UK.

Conclusion

Our findings build on existing movement ecology knowledge for *Z. longissimus* using advanced methodology that simultaneously modelled movement and habitat selection to assess preferences. This study was among the first to use VHF telemetry to study an introduced population of *Z. longissimus* and for a non-native reptile species in the UK. Telemetry revealed snakes exhibited site fidelity and high variability between individual movement patterns. High heterogeneity was present between individuals. We found positive associations and avoidance in distance to habitat selection, and several interactions between step characteristics and habitat features in our analysis of individuals. At a population level, we identified preferences for buildings, hedgerows, and scrub, but step characteristics had no relationship with any habitat feature. The selection of buildings in North Wales has also been documented in northern European populations, indicating snakes could be at their thermoregulatory limit. Behavioural observations made during data collection also aid in our understanding of snake behaviour and interactions in a novel environment. Populations of *Z. longissimus* in the UK should be monitored to react to early warning signs and allow for quick responses toward changes in circumstances. Prioritising habitat snakes are most likely to use will improve detection rates and increase capture probabilities during visual searches and trapping. Our results demonstrate the importance of including individual-level analyses to account for individual heterogeneity which will help inform policymakers and organisations for future mitigation efforts.

Reference list

- Allen, W.L., Street, S.E., and Capellini, I. (2017). Fast life history traits promote invasion success in amphibians and reptiles. *Ecology Letters*, **20**(2): 222-230.
- Allentoft, M.E., Rasmussen, A.R., and Kristensen, H.V. (2018). Centuries-Old DNA from an Extinct Population of Aesculapian Snake (*Zamenis longissimus*) Offers New Phylogeographic Insight. *Diversity*, **10**(1): 1-10
- Avery, M.L., Tillman, E.A., Spurfeld, C., Engeman, R.M., Maciejewski, K.P., Brown, J.D., and Fetzer, E.A. (2014). Invasive Black Spiny-tailed Iguanas (*Ctenosaura similis*) on Gasparilla Island, Florida, USA. *Integrative Zoology*, **9**(5): 590-597.
- Avgar, T., Potts, J.R., Lewis, M.A., and Boyce, M.S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, **7**(5): 619-630.
- Batoszek, I.A., Smith, B.J., Reed, R.N., and Hart, K.M. (2021). Spatial ecology of invasive Burmese pythons in Southwestern Florida. *Ecosphere*, **12**(6): e03564.
- Baxter-Gilbert, J., Riley, J.L., and Measey, J. (2021). Fortune favours the bold toad: urban-derived behavioural traits may provide advantages for the invasive amphibian populations. *Behavioural ecology and sociobiology*, **75**(9): 130.
- Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M., and Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use–availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**(1550): 2245–2254.
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., and Richardson, D.M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**(1): 333–339.
- Boback, S.M., Nafus, M.G., Yackel Adams, A.A., and Reed, R.N. (2020). Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities. *Ecosphere*, **11**(1): e03000

- Borden, J.B., and Flory, S.L. (2021). Urban evolution of invasive species. *Frontiers in Ecology and the Environment*, **19**(3): 184–191.
- Boyle, M., Schwanz, L., Hone, J., and Georges, A. (2016). Dispersal and climate warming determine range shift in model reptile populations. *Ecological Modelling*, **328**(1): 34-43.
- Breining, D.R., Bolt, R.M., Legare, M.L., Drese, J.H., and Stolen, E.D. (2011). Factors influencing home-range sizes of Eastern Indigo snakes in Central Florida. *Journal of Herpetology*, **45**(4): 484-490.
- Buckley, Y.M., and Catford, J. (2015). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, **104**(1): 4-17.
- Capinha, C., Seebens, H., Cassey, P., García-Díaz, P., Lenzner, B., Mang, T., Moser, D., Pyšek, P., Rödder, D., Scalera, R., Winter, M., Dullinger, S., and Essl, F. (2017). Diversity, biogeography and the global flows of alien amphibians and reptiles. *Diversity and Distributions*, **23**(11): 1313-1322.
- Capizzi, D., Capula, M., Rugiero, L., and Luiselli, L. (2008). Dietary patterns of two sympatric Mediterranean snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) along a gradient of habitat alteration. *Herpetological Journal*, **18**(3), 141-146.
- Capula, M., and Luiselli, L. (2002). Feeding strategies of *Elaphe longissima* from contrasting Mediterranean habitats in central Italy. *Italian Journal of Zoology*, **69**(2): 153–156.
- Claunch, N.M., Goodman, C., Reed, R.N., Guralnick, R., Romagosa, C.M., and Taylor, E.N. (2021). Invaders from islands: thermal matching, potential or flexibility? *Biological Journal of the Linnean Society*, **134**(3): 587–603.
- Crane, M., Silva, I., Marshall, B.M., and Strine, C.T. (2021). Lots of movement, little progress: a review of reptile home range literature. *PeerJ*, **9**(1): p.e11742.

- Cuthbert, R.N., Diagne, C., Haubrock, P.J., Turbelin, A.J., and Courchamp, F. (2022). Are the “100 of the world’s worst” invasive species also the costliest? *Biological Invasions*, **24**(1): 1895–1904.
- Daly, E.Z., Chabrierie, O., Massol, F., Facon, B., Hess, M.C.M., Tasiemski, A., Grandjean, F., Chauvat, M., Viard, F., Forey, E., Folcher, L., Buisson, E., Boivin, T., Baltora-Rosset, S., Ulmer, R., Gibert, P., Thiébaud, G., Pantel, J.H., Heger, T., Richardson, D.M., and Renault, D. (2023). A synthesis of biological invasion hypotheses associated with the introduction-naturalisation-invasion continuum. *Oikos*, **2023**(5): e09645
- Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T.M., Dyer, E.E., Cassey, P., Scrivens, S.L., Economo, E.P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwing, W., García-Berthou, E., Casal, C., Mandrak, N.E., Fuller, P., Meyer, C., and Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology Evolution*, **1**(1): 0186.
- Dorcas, M.E., Wilson, J.D., Reed, R.N., Snow, R.W., Rochford, M.R., Miller, M.A., Meshaka, W.E., Andreadis, P.T., Mazzotti, F.J., Romagosa, C.M., and Hart, K.M. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Biological Sciences*, **109**(7): 2418-2422.
- Edgar, P., and Bird, D.R. (2006). Action Plan for the Conservation of the Aesculapian Snake (*Zamenis longissimus*) in Europe. Convention on the Conservation of European Wildlife and Natural Habitats. Council of Europe, Strasbourg, France.
- Febrer-Serra, M., Lassnig, N., Colomar, V., Picó, G., Sureda, A., and Pinya, S. (2023). Demographic monitoring of the invasive ladder snake on Formentera (Balearic Islands, Spain). *Journal of Zoology*, **320**(3): 236–247.
- Feuka, A.B., Nafus, M.G., Yackel Adams, A.A., Bailey, L.L., and Hooten, M.B. (2022). Individual heterogeneity influences the effects of translocation on urban dispersal of an invasive reptile. *Movement Ecology*, **10**(2): 1-18.

- Fieberg, J., Signer, J., Smith, B., and Avgar, T. (2021). A 'How to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, **90**(5): 1027-1043.
- Filz, K.J., Bohr, A., and Lötters, S. (2018). Abandoned Foreigners: is the stage set for exotic pet reptiles to invade Central Europe? *Biodiversity Conservation*, **27**(1): 417–435.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., and Winne, C.T. (2000). The Global Decline of Reptiles, Déjà Vu Amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience*, **50**(8): 653–666.
- Goetz, S.M., Hileman, E.T., Nafus, M.G., Yackel Adams, A.A., Bryant, A.R., Reed, R.N., and Siers, S.R. (2021). Brown Treesnake Mortality After Aerial Application of Toxic Baits. *The Journal of Wildlife Management*, **85**(7): 1507–1514.
- Guiller, G., Legentilhomme, J., Boissinot, A., Blouin-Demers, G., Barbraud, C., and Lourdais, O. (2022). Response of farmland reptiles to agricultural intensification: Collapse of the common adder *Vipera berus* and the western green lizard *Lacerta bilineata* in a hedgerow landscape. *Animal conservation*, **25**(6): 849-864.
- Guzy, J.C., Falk, B.G., Smith, B.J., Willson, J.D., Reed, R.N., Aumen, N.G., Avery, M.L., Bartoszek, I.A., Campbell, E., Cherkiss, M.S., Claunch, N.M., Currylow, A.F., Dean, T., Dixon, J., Engeman, R., Funck, S., Gible, R., Hengstebeck, K.C., Humphrey, J.S., and Hunter, M.E. (2023). Burmese pythons in Florida: A synthesis of biology, impacts, and management tools. *NeoBiota*, **80**(1): 1–119.

- Jeschke, J.M., Bacher, S., Blackburn, T.M., Dick, J.T.A., Essl, F., Evans, T., Gaertner, M., Hulme, P.E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilà, M., Winter, M., and Kumschick, S. (2014). Defining the impact of non-native species. *Conservation Biology*, **28**(5): 1188-1194.
- Karelus, D.L., McCown, J.W., Scheick, B.K., Van de Kerk, M., Bolker, B.M., and Oli, M.K. (2017). Effects of environmental factors and landscape features on movement patterns of Florida black bears. *Journal of Mammalogy*, **98**(5): 1463-1478.
- Keller, R.P., Geist, J., Jeschke, J.M., and Kühn, I. (2011). Invasive species in Europe: ecology, status, and policy. *Environ Sciences Europe*, **23**(23): 1-17.
- Kovar, R., Brabec, M., Vita, R., and Bocek, R. (2014). Mortality rate and activity patterns of an Aesculapian snake (*Zamenis longissimus*) population divided by a busy road. *Journal of Herpetology*, **48**(1): 24-33.
- Kovar, R., Brabec, M., Vita, R., Vodicka, R., and Bogdan, V. (2016). Habitat use of the Aesculapian Snake, *Zamenis longissimus*, at the northern extreme of its range in northwest Bohemia. *The Herpetological Bulletin*, **136**: 1-9.
- Kovar, R., Brabec, M., Vita, R., Vodicka, R., and Bogdan, V. (2016). Nesting and over-wintering sites of Aesculapian snake, *Zamenis longissimus*, in an anthropogenic landscape in the northern extreme of its range. *The Herpetological Bulletin*, **136**(2): 35-36.
- Kunegel-Lion, M., Neilson, E.W., Mansuy, N., and Goodsman, D.W. (2022). Habitat quality does not predict animal population abundance on frequently disturbed landscapes. *Ecological Modelling*, **469**: 109943.
- Kurek, K., Król, W., Najberek, K., Ćmiell, A.M., Solarz, W., Bury, S., Baś, G., Najbar, B., and Okarma, H. (2018). Habitat Use of the Aesculapian Snake at Different Spatial Scales. *The Journal of Wildlife Management*, **82**(8): 1746-1755.
- Kurek, K., Najberek, K., Zając, B., Bury, S., Ćmiell, A.M., Baś, G., and Najbar, B. (2017). Changes in the distribution of the Aesculapian snake in Poland and

- the implication for its active conservation. *Polish Journal of Ecology*, **65**(4): 422-431.
- Langton, T., Atkins, W., and Herbert, C. (2011). On the distribution, ecology and management of non-native reptiles and amphibians in the London Area. Part 1. Distribution and predator/prey impacts. *The London Naturalist*, **90**(1): 83-156.
- Lee, K.H., Chen, T.H., Shang, G., Clulow, S., Yang, Y.J., and Lin, S.M. (2019). A check list and population trends of invasive amphibians and reptiles in Taiwan. *ZooKeys*, **829**(1): 85–130.
- Lelièvre, H., Blouin-Demers, G., Bonnet, X., and Lourdais, O. (2010). Thermal benefits of artificial shelters in snakes: A radiotelemetric study of two sympatric colubrids. *Journal of Thermal Biology*, **35**(7): 324-331.
- Lelièvre, H., Legagneux, P., Blouin-Demers, G., Bonnet, X., and Lourdais, O. (2012a). Trophic niche overlap in two syntopic colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) with contrasted lifestyles. *Amphibia-Reptilia*, **33**(1): 37-44.
- Lelièvre, H., Moreau, C., Blouin-Demers, G., Bonnet, X., and Lourdais, O. (2012b). Two syntopic colubrid snakes differ in their energetic requirements and in their use of space. *Herpetologica*, **68**(3): 358-364.
- Lettoof, D.C., Parkin, T., Jolly, C.J., Laive, A., and Takach, B. (2023). Snake life history traits and their association with urban habitat use in a tropical city. *Urban Ecosystems*, **26**(2): 433-445.
- Lowry, H., Lill, A., and Wong, B.B.M. (2012). Behavioural responses of wildlife to urban environments. *Biological Reviews*, **88**(3): 537-549.
- Luiselli, L., and Rugiero, L. (1993). Food Habits of the Aesculapian Snake, *Elaphe longissima*, in Central Italy: Do Arboreal Snakes Eat More Birds than Terrestrial Ones? *Journal of Herpetology*, **27**(1): 116-117.

- Maag, D. W., Maher, S.P., and Greene, B. (2022). Sexual size monomorphism of a Pygmy Rattlesnake (*Sistrurus miliarius*) population in southwestern Missouri, USA. *Amphibia-Reptilia*, **44**(1): 103–105.
- Maestresalas, B., Piquet, J.C., and López-Darias, M. (2023). Spatial ecology to strengthen invasive snake management on islands. *Scientific Reports*, **13**: 6731
- Manchester, S.J., and Bullock, J.M. (2001). The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology*, **37**(5): 845–864.
- Marshall, B.M., Crane, M., Silva, I., Strine, C.T., Jones, M.D., Hodges, C.W., Suwanwaree, P., Artchawakom, T., Waengsothorn, S., and Goode, M. (2020). No room to roam: King Cobras reduce movement in agriculture. *Movement Ecology*, **8**(1): 33.
- Martin, A.R., and Lea, V.J. (2020). A mink-free GB: perspectives on eradicating American mink *Neovision vison* from Great Britain and its islands. *Mammal Review*, **50**(2): 170-179.
- Martin, P.A., Shackelford, G.E., Bullock, J.M., Gallardo, B., Aldridge, D.C., and Sutherland, W.J. (2020). Management of UK priority invasive alien plants: a systematic review protocol. *Environmental Evidence*, **9**(11): 1-14.
- Matthias, L., Allison, M.J., Maslovat, C.Y., Hobbs, J., and Helbing, C.C. (2021). Improving ecological surveys for the detection of cryptic, fossorial snakes using eDNA on and under artificial cover objects. *Ecological Indicators*, **131**: 108187.
- Meek, R. (2017). Repeated use of roadside tunnels of the European mole (*Talpa europea*) as a communal nesting area by grass snakes, *Natrix natrix*: are there thermal benefits? *The Herpetological Bulletin*, **139**(1): 16-19.
- Mercker, M., Schwemmer, P., Peschko, V., Enners, L., and Garthe, S. (2021). Analysis of local habitat selection and large-scale attraction/avoidance based

- on animal tracking data: is there a single best method? *Movement Ecology*, **9**(1): 20.
- Mole, S.R.C. (2010). Changes in relative abundance of the western green lizard *Lacerta bilineata* and the common wall lizard *Podarcis muralis* introduced onto Boscombe Cliffs, Dorset, UK. *The Herpetological Bulletin*, **114**(4): 24-29.
- Montes, E., Kraus, F., Chergui, B., and Pleguezuelos, J.M. (2021). Collapse of the endemic lizard *Podarcis pityusensis* on the island of Ibiza mediated by an invasive snake. *Current Zoology*, **68**(3): 295-303.
- Muff, S., Signer, J., and Fieberg, J. (2019). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, **89**(1): 80-92.
- Musilová, R., Zavadil, V., and Kotlík, P. (2007). Isolated populations of *Zamenis longissimus* (Reptilia: Squamata) above the northern limit of the continuous range in Europe: origin and conservation status. *Acta Societatis Zoologicae Bohemicae*, **71**: 197-208.
- Musilová, R., Zavadil, V., Marková, S., and Kotlík, P. (2010). Relics of the Europe's warm past: Phylogeography of the Aesculapian snake. *Molecular phylogenetics and evolution*, **57**(3): 1245-1252.
- Nafus, M.G., Siers, S.R., Levine, B.A., Quiogue, Z.C., and Yackel Adams, A.A. (2021). Demographic response of brown treesnakes to extended population suppression. *The Journal of Wildlife Management*, **86**(1): e22136.
- Nafus, M.G., Yackel, A.A., Klug, P.E., and Rodda, G.H. (2018). Habitat type and structure affect trap capture success of an invasive snake across variable densities. *Ecosphere*, **9**(8): e02339
- Najbar, B. (2007). Food habits of *Zamenis longissimus* (Laurenti, 1768) (Reptilia: Serpentes: Colubridae) in Bieszczady (south-eastern Poland). *Vertebrate Zoology*, **57**(1): 73-77.

- NNSS. 2023. GB non-native species secretariat. [online]. www.nonnativespecies.org. Accessed 26th October 2023.
- Northrup, J.M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M.P., Leclerc, M., Prokopenko, C.M., and Gerber, B.D. (2022). Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. *Ecological Applications*, **32**(1): e02470.
- Pauwels, O.S.G., and Pantchev, N. (2018). Risks for human health related to invasive alien reptiles and amphibians. *CABI eBooks*: 108-119.
- Piquet, J.C., and López-Darias, M. (2021). Invasive snake causes massive reduction of all endemic herpetofauna on Gran Canaria. *Proceedings of the Royal Society B: Biological Sciences*, **288**(1964): 20211939.
- Piquet, J.C., Warren, D.L., Saavedra Bolaños, J.F., Sánchez Rivero, J.M., Gallo-Barneto, R., Cabrera-Pérez, M.Á., Fisher, R.N., Fisher, S.R., Rochester, C.J., Hinds, B., Nogales, M., and López-Darias, M. (2021). Could climate change benefit invasive snakes? Modelling the potential distribution of the California Kingsnake in the Canary Islands. *Journal of Environmental Management*, **294**: 112917.
- Polce, C., Cardoso, A.C., Deriu, I., Gervasini, E., Tsiamis, K., Vigiak, O., Zulian, G., and Maes, J. (2023). Invasive alien species of policy concerns show widespread patterns of invasion and potential pressure across European ecosystems. *Scientific Reports*, **13**(1): 8124.
- Pulsford, S.A., Driscoll, D.A., Barton, P.S., and Lindenmayer, D.B. (2017). Remnant vegetation, plantings and fences are beneficial for reptiles in agricultural landscapes. *Journal of Applied Ecology*, **54**(6): 1710-1719.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., and Kleunen, M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, **95**(6): 1511–1534.

- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- R Studio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. <http://www.rstudio.com/>.
- Reinert, H.K., and Cundall, D. (1982). An Improved Surgical Implantation Method for Radio-Tracking Snakes. *Copeia*, **1982**(3): 702-705.
- Reiřek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebald, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., and Richardson, D.M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, **95**(6): 1511-1534.
- Ricciardi, A., and Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, **9**(1): 309-315.
- Rodda, G.H., and Fritts, T.H. (1992). The Impact of the Introduction of the Colubrid Snake *Boiga irregularis* on Guam's Lizards. *Journal of Herpetology*, **26**(2): 166-174.
- Rollins, L.A., Richardson, M.F., and Shine, R. (2015). A genetic perspective on rapid evolution in cane toads (*Rhinella marina*). *Molecular Ecology*, **24**(9): 2264-2276.
- Roy, H.E., Peyton, J., Aldridge, D.C., Bantock, T., Blackburn, T.M., Britton, R., Clark, P., Cook, E., Dehnen-Schmutz, K., Dines, T., Dobson, M., Edwards, F., Harrower, C., Harvey, M.C., Minchin, D., Noble, D.G., Parrott, D., Pocock, M.J.O., Preston, C.D., Roy, S., Salisbury, A., Schönrogge, K., Sewell, J., Shaw, R.H., Stebbing, P., Stewart, A.J.A., and Walker, K.J. (2014). Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biology*, **20**(12): 3859-3871.

- Rue, H., Martino, S., and Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B Statistics Methodology*, **71**(2): 319–392.
- Rugiero, L., and Luiselli, L. (2004). Ecological notes on two colubrid snakes (*Coluber viridiflavus* and *Elaphe longissima*) in a suburban habitat (Rome, central Italy). *Herpetological Bulletin*, **87**: 8-12.
- Rugiero, L., Capizzi, D., and Luiselli, L. (2002). Interactions between sympatric snakes, *Coluber viridiflavus* and *Elaphe longissima*: are there significant inter-annual differences in coexistence patterns? *Ecologia mediterranea*, **28**(2): 75–91.
- Rugiero, L., Luiselli, L., Capula, M., Petrozzi, F., Di Vittorio, M., Pacini, N., Vignoli, L., Dendi, D., Milana, G., Amori, G., and Meek, R. (2020). Snakes and the Eternal City: variation in community metrics, body size and population density of snakes in contrasted landscapes of suburban Rome (Italy). *Herpetological Journal*, **30**(2): 69-82.
- Rutz, C., and Webster, M.M. (2021). Ethology adopts the STRANGE framework for animal behaviour research, to improve reporting standards. *Ethology*, **127**(2): 99-101.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., and Kartesz, J. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, **8**(1): 14435.
- Signer, J., Fieberg, J., and Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, **9**(2): 880–890.

- Silva-Rocha, I., Santos, J.M., Rocha, R., and Rato, C. (2022). Bioclimatic and local drivers modulating the expansion of an introduced temperate reptile in a subtropical island. *Global Ecology and Conservation*, **37**: 02164.
- Smith, S.N., Jones, M.D., Marshall, B.M. (2021). Native Burmese pythons exhibit site fidelity and preference for aquatic habitats in an agricultural mosaic. *Scientific Reports*, **11**: 7014.
- Speybroeck, J., Beukema, W., Bok, B., and Van, J. (2016). *Field Guide to the Amphibians and Reptiles of Britain and Europe*. Bloomsbury Publishing.
- Steele, Z.T. (2023). A review of common factors among successful and failed efforts to eradicate invasive vertebrates in Florida. *Southeastern Naturalist*, **22**(2): 222-253.
- Street, S.E., Gutiérrez, J.S., Allen, W.L., and Capellini, I. (2023). Human activities favour prolific life histories in both traded and introduced vertebrates. *Nature Communications*, **14**(1): 262
- Stroh, P.A., Walker, K.J., Humphrey, T.A., Pescott, O.L., and Burkmar, R.J. (2023). *Plant Atlas 2020*. Princeton University Press.
- Tedeschi, L., Biancolini, D., Capinha, C., Rondinini, C., and Essl, F. (2021). Introduction, spread, and impacts of invasive alien mammal species in Europe. *Mammal Review*, **52**(2): 252-266.
- Thurjfell, H., Ciuti, S., and Boyce, M.S. (2014). Applications of step-select functions in ecology and conservation. *Movement Ecology*, **2**(4): 1-12.
- Veitch, C.R., Clout, M.N., Martin, A.R., Russell, J.C., and West, C.J. (2019). Island invasives: scaling up to meet the challenge. Proceedings of the international conference on island invasives 2017. *International Union for Conservation of Nature*, **62**: 317-355.
- Vilizzi, L., Copp, G.H., Hill, J.E., Adamovich, B., Aislabie, L., Akin, D., Al-Faisal, A.J., Almeida, D., Azmai, M.N.A., Bakiu, R., Bellati, A., Bernier, R., Bies, J.M., Bilge, G., Branco, P., Bui, T.D., Canning-Clode, J., Cardoso Ramos, H.A., Castellanos-Galindo, G.A., Castro, N., Chaichana, R., Chainho, P., Chan, J.,

Cunico, A.M., Curd, A., Dangchana, P., Dashinov, D., Davison, P.I., de Camargo, M.P., Dodd, J.A., Durland Donahou, A.L., Edsman, L., Ekmekçi, F.G., Elphinstone-Davis, J., Erős, T., Evangelista, C., Fenwick, G., Ferincz, Á., Ferreira, T., Feunteun, E., Filiz, H., Forneck, S.C., Gajduchenko, H.S., Gama Monteiro, J., Gestoso, I., Giannetto, D., Gilles, A.S., Gizzi, F., Glamuzina, B., Glamuzina, L., Goldsmit, J., Gollasch, S., Gouletquer, P., Grabowska, J., Harmer, R., Haubrock, P.J., He, D., Hean, J.W., Herczeg, G., Howland, K.L., İlhan, A., Interesova, E., Jakubčinová, K., Jelmert, A., Johnsen, S.I., Kakareko, T., Kanongdate, K., Killi, N., Kim, J.E., Kırankaya, Ş.G., Kňazovická, D., Kopecký, O., Kostov, V., Koutsikos, N., Kozic, S., Kuljanishvili, T., Kumar, B., Kumar, L., Kurita, Y., Kurtul, I., Lazzaro, L., Lee, L., Lehtiniemi, M., Leonardi, G., Leuven, R.S.E.W., Li, S., Lipinskaya, T., Liu, F., Lloyd, L., Lorenzoni, M., Luna, S.A., Lyons, T.J., Magellan, K., Malmstrøm, M., Marchini, A., Marr, S.M., Masson, G., Masson, L., McKenzie, C.H., Memedemin, D., Mendoza, R., Minchin, D., Miossec, L., Moghaddas, S.D., Moshobane, M.C., Mumladze, L., Naddafi, R., Najafi-Majd, E., Năstase, A., Năvodaru, I., Neal, J.W., Nienhuis, S., Nimtim, M., Nolan, E.T., Occhipinti-Ambrogi, A., Ojaveer, H., Olenin, S., Olsson, K., Onikura, N., O'Shaughnessy, K., Paganelli, D., Parretti, P., Patoka, J., Pavia, R.T.B Jr., Pellitteri-Rosa, D., Pelletier-Rousseau, M., Peralta, E.M., Perdikaris, C., Pietraszewski, D., Piria, M., Pitois, S., Pompei, L., Poulet, N., Preda, C., Puntilla-Dodd, R., Qashqaei, A.T., Radočaj, T., Rahmani, H., Raj, S., Reeves, D., Ristovska, M., Rizevsky, V., Robertson, D.R., Robertson, P., Ruykys, L., Saba, A.O., Santos, J.M., Sarı, H.M., Segurado, P., Semenchenko, V., Senanan, W., Simard, N., Simonović, P., Skóra, M.E., Slovák Švolíková, K., Smeti, E., Šmídová, T., Špelić, I., Srébalienė, G., Stasolla, G., Stebbing, P., Števo, B., Suresh, V.R., Szajbert, B., Ta, K.A.T., Tarkan, A.S., Tempesti, J., Therriault, T.W., Tidbury, H.J., Top-Karakuş, N., Tricarico, E., Troca, D.F.A., Tsiamis, K., Tuckett, Q.M., Tutman, P., Uyan, U., Uzunova, E., Vardakas, L., Velle, G., Verreycken, H., Vintsek, L., Wei, H., Weiperth, A., Weyl, O.L.F., Winter, E.R., Włodarczyk, R., Wood, L.E., Yang, R., Yapıcı, S., Yeo, S.S.B., Yoğurtçuoğlu, B., Yunnice, A.L.E., Zhu, Y., Zięba, G., Žitňanová, K., and Clarke, S. (2021). A global-scale screening of non-native

- aquatic organisms to identify potentially invasive species under current and future climate conditions. *Science of The Total Environment*, **788**: 147868.
- Vindenes, Y., and Langangen, Ø. (2015). Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecology Letter*, **18**(5): 417-432.
- Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., and Bugmann, H. (2009). Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, **24**(12): 686–693.
- Webster, M.M., and Rutz, C. (2020). How STRANGE are your study animals? *Nature*, **582**(7812): 337–340.
- While, G.M., Williamson, J., Prescott, G., Horváthová, T., Fresnillo, B., Beeton, N.J., Halliwell, B., Michaelides, S., and Uller, T. (2015). Adaptive responses to cool climate promotes persistence of a non-native lizard. *Proceedings of the Royal Society B*, **282**: 1803.
- Whiting, M.J., Dixon, J.R., and Greene, B.D. (1996). Measuring snake activity patterns: The influence of habitat heterogeneity on catchability. *Amphibia-Reptilia*, **17**(1): 47-54.
- Wiles, G.J., Bart, J., Beck, R.E., and Aguon, C.F. (2003). Impacts of the Brown Tree Snake: Patterns of Decline and Species Persistence in Guam's Avifauna. *Conservation Biology*, **17**(5): 1350–1360.
- Wilson, J.D. (2017). Indirect effects of invasive Burmese pythons on ecosystems in southern Florida. *Journal of Applied Ecology*, **54**(4): 1251-1258.
- Yan, X., Zhenyu, L., Gregg, W.P., and Dianmo, L. (2001). Invasive species in China – an overview. *Biodiversity and Conservation*, **10**(1): 1317-1341.
- Yu, X., Wu, N.C., Ge, L., Li, L., Zhang, Z., and Lei, J. (2022). Artificial shelters provide suitable thermal habitat for a cold-blooded animal. *Scientific Reports*, **12**(1): 5879.

Appendices

Appendix table 1. Capture and release summary for all Aesculapian snakes. The capture date and time, location, method of capture and release date and time are included.

Snake ID	Capture date	Capture time	Capture latitude	Capture longitude	Method	Release date	Release time
M031	03/06/2022	14:33	53.29371	-3.74650	Opportunistic	07/06/2022	15:18
M074	12/07/2022	10:01	53.29729	-3.74871	Opportunistic	15/07/2022	10:10
M154	15/06/2022	10:12	53.29322	-3.75199	Opportunistic	17/06/2022	11:36
M202	08/05/2022	14:01	53.29574	-3.75853	Survey	11/05/2022	09:57
M209	20/05/2022	15:21	53.29424	-3.74877	Member of public/zoo staff	25/05/2022	10:08
M217	11/06/2022	09:25	53.29802	-3.74999	Opportunistic	14/06/2022	10:00
M218	21/06/2022	11:44	53.29308	-3.75208	Opportunistic	24/06/2022	15:03

Appendix table 2. All results from the individual Integrated step selection analysis for all Aesculapian snakes (*Zamenis longissimus*) tracked in Colwyn Bay, North Wales. Abbreviations for sl: step length, ta: turn angle.

Term	Estimate	Standard error	Statistic	P value	Confidence Interval (lower)	Confidence interval (upper)	ID	Model	AIC score
log_sl	0.0374208	0.170698491	0.219221	0.826478	-0.297142	0.3719837	M031	model1	259.23847
cos_ta	0.262913	0.693251655	0.379246	0.704505	-1.095835	1.6216612	M031	model1	259.23847
log_sl:cos_ta	-0.189933	0.230987272	-0.82227	0.410925	-0.64266	0.2627937	M031	model1	259.23847
dist_Meadow	-10.57507	10.95335179	-0.96546	0.334313	-32.04324	10.893109	M031	model2	264.19176
log_sl	-14.14458	15.36100007	-0.92081	0.357149	-44.25159	15.962425	M031	model2	264.19176
cos_ta	1.4378636	27.13800052	0.052983	0.957745	-51.75164	54.627367	M031	model2	264.19176
dist_Meadow:log_sl	2.3321312	2.525571535	0.923407	0.355795	-2.617898	7.2821604	M031	model2	264.19176
dist_Meadow:cos_ta	-0.198261	4.479848738	-0.04426	0.9647	-8.978603	8.582081	M031	model2	264.19176
log_sl:cos_ta	-0.178624	0.238567095	-0.74874	0.454015	-0.646207	0.2889584	M031	model2	264.19176
dist_Pasture	2.5047276	6.288193302	0.398322	0.690393	-9.819905	14.82936	M031	model3	264.63385
log_sl	1.1802653	8.175600679	0.144364	0.885213	-14.84362	17.204148	M031	model3	264.63385
cos_ta	-4.094132	13.97389643	-0.29298	0.769534	-31.48247	23.294201	M031	model3	264.63385
dist_Pasture:log_sl	-0.205263	1.459165734	-0.14067	0.88813	-3.065175	2.6546494	M031	model3	264.63385
dist_Pasture:cos_ta	0.7795974	2.497157164	0.312194	0.754893	-4.114741	5.6739355	M031	model3	264.63385
log_sl:cos_ta	-0.19829	0.230313371	-0.86096	0.389262	-0.649696	0.2531163	M031	model3	264.63385
dist_Hedge	3.4407866	6.745368877	0.510096	0.609984	-9.779893	16.661467	M031	model4	264.97708
log_sl	4.117121	9.313574426	0.442056	0.658449	-14.13715	22.371391	M031	model4	264.97708
cos_ta	1.6351879	16.62743316	0.098343	0.92166	-30.95398	34.224358	M031	model4	264.97708
dist_Hedge:log_sl	-0.722091	1.644392948	-0.43912	0.660572	-3.945042	2.5008599	M031	model4	264.97708
dist_Hedge:cos_ta	-0.244024	2.940786162	-0.08298	0.933868	-6.007859	5.5198106	M031	model4	264.97708
log_sl:cos_ta	-0.188116	0.231550716	-0.81242	0.416552	-0.641947	0.2657153	M031	model4	264.97708
dist_Woodland	-1.033671	7.520461635	-0.13745	0.890677	-15.7735	13.706163	M031	model5	264.63944
log_sl	-1.0634	10.54440033	-0.10085	0.91967	-21.73005	19.603245	M031	model5	264.63944
cos_ta	12.624445	17.30845128	0.72938	0.465769	-21.2995	46.548386	M031	model5	264.63944

dist_Woodland:log_sl	0.203739	1.962845921	0.103798	0.91733	-3.643368	4.0508464	M031	model5	264.63944
dist_Woodland:cos_ta	-2.306701	3.225824975	-0.71507	0.474564	-8.629202	4.0157995	M031	model5	264.63944
log_sl:cos_ta	-0.180033	0.231717626	-0.77695	0.437187	-0.634192	0.2741249	M031	model5	264.63944
dist_Scrub	2.366487	9.428906838	0.250982	0.801828	-16.11383	20.846805	M031	model6	264.94755
log_sl	1.0582464	13.23028114	0.079987	0.936248	-24.87263	26.989121	M031	model6	264.94755
cos_ta	-6.956316	23.07380065	-0.30148	0.763048	-52.18013	38.267502	M031	model6	264.94755
dist_Scrub:log_sl	-0.170912	2.196756267	-0.0778	0.937985	-4.476476	4.1346508	M031	model6	264.94755
dist_Scrub:cos_ta	1.2004205	3.837790661	0.312789	0.754441	-6.321511	8.722352	M031	model6	264.94755
log_sl:cos_ta	-0.194935	0.22999323	-0.84757	0.396679	-0.645713	0.2558439	M031	model6	264.94755
dist_Gardens	-43.01727	20.62410299	-2.08578	0.036999	-83.43977	-2.5947755	M031	model7	256.57759
log_sl	-52.5699	27.87734687	-1.88576	0.059328	-107.2085	2.0686935	M031	model7	256.57759
cos_ta	99.910951	67.72177667	1.475315	0.140128	-32.82129	232.64319	M031	model7	256.57759
dist_Gardens:log_sl	9.762132	5.176945201	1.885694	0.059336	-0.384494	19.908758	M031	model7	256.57759
dist_Gardens:cos_ta	-18.50098	12.56319376	-1.47263	0.14085	-43.12439	6.1224272	M031	model7	256.57759
log_sl:cos_ta	-0.110186	0.229110168	-0.48093	0.630565	-0.559234	0.3388612	M031	model7	256.57759
dist_Buildings	17.005582	17.24678285	0.986015	0.324126	-16.79749	50.808655	M031	model8	251.9706
log_sl	-3.019537	29.17044655	-0.10351	0.917555	-60.19256	54.153488	M031	model8	251.9706
cos_ta	-68.86693	48.34865902	-1.42438	0.154336	-163.6286	25.894697	M031	model8	251.9706
dist_Buildings:log_sl	0.588664	5.327899758	0.110487	0.912023	-9.853828	11.031156	M031	model8	251.9706
dist_Buildings:cos_ta	12.614259	8.820348657	1.430132	0.152679	-4.673306	29.901825	M031	model8	251.9706
log_sl:cos_ta	-0.15249	0.261196242	-0.58381	0.559345	-0.664425	0.3594451	M031	model8	251.9706
dist_Road_Surface	-10.11482	9.295217822	-1.08817	0.276518	-28.33311	8.1034711	M031	model9	262.26605
log_sl	-7.173041	11.51373655	-0.623	0.533285	-29.73955	15.393467	M031	model9	262.26605
cos_ta	0.3934118	18.76662566	0.020963	0.983275	-36.3885	37.175322	M031	model9	262.26605
dist_Road_Surface:log_sl	1.3160566	2.097593156	0.627413	0.530389	-2.79515	5.4272637	M031	model9	262.26605
dist_Road_Surface:cos_ta	-0.020808	3.410205198	-0.0061	0.995132	-6.704687	6.6630718	M031	model9	262.26605
log_sl:cos_ta	-0.202042	0.230604648	-0.87614	0.380955	-0.654018	0.2499352	M031	model9	262.26605
log_sl	0.0210227	0.147188814	0.142828	0.886426	-0.267462	0.3095075	M154	model1	511.0218
cos_ta	-1.31521	0.659892662	-1.99307	0.046254	-2.608575	-0.0218437	M154	model1	511.0218
log_sl:cos_ta	0.3997599	0.202090809	1.97812	0.047915	0.0036692	0.7958506	M154	model1	511.0218

dist_Meadow	-17.33403	10.81203921	-1.60322	0.108887	-38.52523	3.8571812	M154	model2	513.98055
log_sl	-17.75602	13.87885021	-1.27936	0.200771	-44.95807	9.4460266	M154	model2	513.98055
cos_ta	-7.00446	22.07615179	-0.31729	0.751026	-50.27292	36.264003	M154	model2	513.98055
dist_Meadow:log_sl	2.7778849	2.173527715	1.278054	0.201231	-1.482151	7.0379209	M154	model2	513.98055
dist_Meadow:cos_ta	0.9126902	3.451608914	0.264425	0.791453	-5.852339	7.6777194	M154	model2	513.98055
log_sl:cos_ta	0.3596398	0.19814401	1.815042	0.069517	-0.028715	0.7479949	M154	model2	513.98055
dist_Pasture	11.33315	8.453828349	1.340594	0.180052	-5.23605	27.902349	M154	model3	510.81446
log_sl	7.3275377	13.44881659	0.544846	0.585859	-19.03166	33.686734	M154	model3	510.81446
cos_ta	1.3133893	18.37145844	0.071491	0.943007	-34.69401	37.320786	M154	model3	510.81446
dist_Pasture:log_sl	-1.218444	2.238351988	-0.54435	0.586201	-5.605533	3.1686451	M154	model3	510.81446
dist_Pasture:cos_ta	-0.42958	3.056576599	-0.14054	0.888231	-6.42036	5.5612001	M154	model3	510.81446
log_sl:cos_ta	0.3651638	0.201323939	1.813812	0.069707	-0.029424	0.7597515	M154	model3	510.81446
dist_Hedge	32.479	18.49981088	1.75564	0.07915	-3.779963	68.737963	M154	model4	500.17514
log_sl	25.157854	30.62051661	0.821601	0.411304	-34.85726	85.172964	M154	model4	500.17514
cos_ta	10.437577	40.36907684	0.258554	0.79598	-68.68436	89.559514	M154	model4	500.17514
dist_Hedge:log_sl	-4.166259	5.102944816	-0.81644	0.414247	-14.16785	5.835329	M154	model4	500.17514
dist_Hedge:cos_ta	-1.979167	6.703102632	-0.29526	0.767794	-15.11701	11.158673	M154	model4	500.17514
log_sl:cos_ta	0.406028	0.217152369	1.869784	0.061514	-0.019583	0.8316388	M154	model4	500.17514
dist_Woodland	0.0437154	4.621013924	0.00946	0.992452	-9.013305	9.1007362	M154	model5	514.33393
log_sl	3.4366348	6.505741291	0.528246	0.597328	-9.314384	16.187653	M154	model5	514.33393
cos_ta	-7.235681	9.442726336	-0.76627	0.443515	-25.74308	11.271723	M154	model5	514.33393
dist_Woodland:log_sl	-0.641444	1.230818366	-0.52115	0.602261	-3.053804	1.7709158	M154	model5	514.33393
dist_Woodland:cos_ta	1.1150809	1.790080085	0.622922	0.533336	-2.393412	4.6235734	M154	model5	514.33393
log_sl:cos_ta	0.4137277	0.20639656	2.004528	0.045014	0.0091978	0.8182575	M154	model5	514.33393
dist_Scrub	1.9854741	15.22649253	0.130396	0.896253	-27.8579	31.828851	M154	model6	504.34164
log_sl	-21.76949	26.18409316	-0.8314	0.405747	-73.08937	29.550394	M154	model6	504.34164
cos_ta	-65.13942	37.75019101	-1.72554	0.08443	-139.1284	8.8495906	M154	model6	504.34164
dist_Scrub:log_sl	3.4513911	4.137341279	0.834205	0.404165	-4.657649	11.560431	M154	model6	504.34164
dist_Scrub:cos_ta	10.087472	5.960144765	1.692488	0.090553	-1.594197	21.769141	M154	model6	504.34164
log_sl:cos_ta	0.3590946	0.219241841	1.637893	0.101444	-0.070612	0.7888007	M154	model6	504.34164

dist_Gardens	8.8316144	3.752228858	2.353698	0.018588	1.477381	16.185848	M154	model7	501.33093
log_sl	5.8485763	5.380954632	1.086903	0.27708	-4.697901	16.395054	M154	model7	501.33093
cos_ta	-2.834632	7.04674536	-0.40226	0.687492	-16.646	10.976736	M154	model7	501.33093
dist_Gardens:log_sl	-1.102451	1.016037606	-1.08505	0.2779	-3.093848	0.8889462	M154	model7	501.33093
dist_Gardens:cos_ta	0.3085573	1.312124114	0.235159	0.814086	-2.263159	2.8802733	M154	model7	501.33093
log_sl:cos_ta	0.3258301	0.205883029	1.582598	0.113513	-0.077693	0.7293534	M154	model7	501.33093
dist_Buildings	8.424952	3.216302448	2.619453	0.008807	2.121115	14.728789	M154	model8	500.65019
log_sl	5.8903579	4.63238022	1.271562	0.203529	-3.18894	14.969656	M154	model8	500.65019
cos_ta	-2.909773	6.308350052	-0.46126	0.644614	-15.27391	9.454366	M154	model8	500.65019
dist_Buildings:log_sl	-1.099459	0.866260773	-1.2692	0.204369	-2.797299	0.5983805	M154	model8	500.65019
dist_Buildings:cos_ta	0.3340524	1.158722248	0.288294	0.773122	-1.937001	2.6051063	M154	model8	500.65019
log_sl:cos_ta	0.2908834	0.204799393	1.420333	0.155511	-0.110516	0.6922829	M154	model8	500.65019
dist_Road_Surface	5.9329556	2.641285225	2.246238	0.024689	0.7561317	11.10978	M154	model9	510.04466
log_sl	5.3498817	3.464135767	1.544363	0.122501	-1.4397	12.139463	M154	model9	510.04466
cos_ta	-4.697663	4.741361834	-0.99078	0.321791	-13.99056	4.5952357	M154	model9	510.04466
dist_Road_Surface:log_sl	-1.002985	0.645235989	-1.55445	0.120078	-2.267624	0.2616542	M154	model9	510.04466
dist_Road_Surface:cos_ta	0.6563262	0.870751553	0.753747	0.451001	-1.050316	2.3629679	M154	model9	510.04466
log_sl:cos_ta	0.3372583	0.199222404	1.692873	0.09048	-0.05321	0.727727	M154	model9	510.04466
log_sl	0.060347	0.074041295	0.815046	0.415046	-0.084771	0.2054653	M202	model1	1043.6041
cos_ta	0.3978395	0.350848497	1.133935	0.256822	-0.289811	1.0854899	M202	model1	1043.6041
log_sl:cos_ta	-0.127664	0.101156845	-1.26204	0.206933	-0.325928	0.0705994	M202	model1	1043.6041
dist_Meadow	-19.07802	21.69369686	-0.87943	0.37917	-61.59688	23.440849	M202	model2	1027.246
log_sl	-62.88333	35.16254376	-1.78836	0.073718	-131.8007	6.0339869	M202	model2	1027.246
cos_ta	-1.011543	52.14187915	-0.0194	0.984522	-103.2077	101.18466	M202	model2	1027.246
dist_Meadow:log_sl	9.81677	5.475772123	1.792765	0.073011	-0.915546	20.549086	M202	model2	1027.246
dist_Meadow:cos_ta	0.2342658	8.121441385	0.028845	0.976988	-15.68347	16.151998	M202	model2	1027.246
log_sl:cos_ta	-0.167303	0.110166459	-1.51864	0.128854	-0.383225	0.0486194	M202	model2	1027.246
dist_Pasture	0.8175264	1.16164451	0.703766	0.481578	-1.459255	3.0943078	M202	model3	1045.254
log_sl	-0.633574	1.287793255	-0.49198	0.62273	-3.157603	1.8904541	M202	model3	1045.254
cos_ta	2.4886309	2.672324033	0.931261	0.351719	-2.749028	7.7262898	M202	model3	1045.254

dist_Past ure:log_sl	0.1227639	0.229315359	0.53535	0.592408	-0.326686	0.5722137	M202	model3	1045.254
dist_Past ure:cos_ta	-0.377746	0.473874454	-0.79714	0.425367	-1.306523	0.5510307	M202	model3	1045.254
log_sl:co s_ta	-0.110309	0.101594136	-1.08578	0.277578	-0.309429	0.0888123	M202	model3	1045.254
dist_Hed gerow	-1.200914	7.202586329	-0.16673	0.86758	-15.31772	12.915896	M202	model4	1040.6336
log_sl	-12.55392	10.88965788	-1.15283	0.24898	-33.89726	8.7894137	M202	model4	1040.6336
cos_ta	-3.407916	21.59108726	-0.15784	0.874584	-45.72567	38.909838	M202	model4	1040.6336
dist_Hed gerow:lo g_sl	2.1184156	1.822981845	1.162061	0.245211	-1.454563	5.6913944	M202	model4	1040.6336
dist_Hed gerow:co s_ta	0.6455053	3.609285358	0.178846	0.858059	-6.428564	7.7195746	M202	model4	1040.6336
log_sl:co s_ta	-0.145469	0.105859631	-1.37417	0.16939	-0.35295	0.0620122	M202	model4	1040.6336
dist_Woo dland	-2.504302	0.981124299	-2.55248	0.010696	-4.42727	-0.5813332	M202	model5	1037.5595
log_sl	-1.048087	0.924564326	-1.1336	0.256962	-2.8602	0.7640256	M202	model5	1037.5595
cos_ta	-0.301623	1.789410221	-0.16856	0.866143	-3.808802	3.2055571	M202	model5	1037.5595
dist_Woo dland:log _sl	0.2373135	0.191417348	1.23977	0.21506	-0.137858	0.6124846	M202	model5	1037.5595
dist_Woo dland:cos _ta	0.1518514	0.367931681	0.412716	0.679815	-0.569281	0.8729842	M202	model5	1037.5595
log_sl:co s_ta	-0.13759	0.104251104	-1.31979	0.186905	-0.341918	0.0667388	M202	model5	1037.5595
dist_Scru b	-2.927691	3.288434555	-0.8903	0.373305	-9.372904	3.5175221	M202	model6	1041.7746
log_sl	-8.962713	4.497184822	-1.99296	0.046266	-17.77703	-0.1483927	M202	model6	1041.7746
cos_ta	-5.152028	8.932248878	-0.57679	0.564082	-22.65891	12.354858	M202	model6	1041.7746
dist_Scru b:log_sl	1.4548664	0.724128269	2.009128	0.044524	0.0356011	2.8741317	M202	model6	1041.7746
dist_Scru b:cos_ta	0.900436	1.437861514	0.626233	0.531162	-1.917721	3.7185928	M202	model6	1041.7746
log_sl:co s_ta	-0.151923	0.104058596	-1.45998	0.144296	-0.355874	0.052028	M202	model6	1041.7746
dist_Gard ens	6.378805	2.435648107	2.618935	0.00882	1.6050224	11.152588	M202	model7	1034.5018
log_sl	4.8760416	2.881661037	1.692094	0.090628	-0.77191	10.523993	M202	model7	1034.5018
cos_ta	12.43694	5.774394728	2.153808	0.031255	1.1193347	23.754546	M202	model7	1034.5018
dist_Gard ens:log_s l	-0.901297	0.541132864	-1.66557	0.095798	-1.961898	0.1593036	M202	model7	1034.5018
dist_Gard ens:cos_t a	-2.244564	1.075026653	-2.08791	0.036806	-4.351578	-0.1375507	M202	model7	1034.5018
log_sl:co s_ta	-0.174316	0.102739387	-1.69668	0.089758	-0.375681	0.0270499	M202	model7	1034.5018
dist_Build ings	9.1584939	2.437009157	3.758088	1.71E-04	4.3820437	13.934944	M202	model8	1019.9671
log_sl	6.6386208	2.921562982	2.272284	0.023069	0.9124626	12.364779	M202	model8	1019.9671
cos_ta	19.082265	6.440792588	2.96272	0.003049	6.4585432	31.705986	M202	model8	1019.9671

dist_Buildings:log_sl	-1.213955	0.539254286	-2.25117	0.024375	-2.270874	-0.1570359	M202	model8	1019.9671
dist_Buildings:cos_ta	-3.439015	1.181861048	-2.90983	0.003616	-5.755421	-1.1226103	M202	model8	1019.9671
log_sl:cos_ta	-0.185525	0.099421634	-1.86604	0.062035	-0.380388	0.0093377	M202	model8	1019.9671
dist_Road_Surface	3.9238311	1.884747108	2.081887	0.037353	0.2297946	7.6178675	M202	model9	1042.3623
log_sl	4.0035088	2.050463189	1.95249	0.05088	-0.015325	8.0223428	M202	model9	1042.3623
cos_ta	5.4766734	3.278107851	1.670681	0.094785	-0.9483	11.901647	M202	model9	1042.3623
dist_Road_Surface:log_sl	-0.727792	0.377021151	-1.93038	0.05356	-1.46674	0.0111556	M202	model9	1042.3623
dist_Road_Surface:cos_ta	-0.92986	0.59752671	-1.55618	0.119665	-2.100991	0.2412704	M202	model9	1042.3623
log_sl:cos_ta	-0.140596	0.099791974	-1.40889	0.158866	-0.336185	0.0549923	M202	model9	1042.3623
log_sl	0.0196292	0.099152856	0.19797	0.843069	-0.174707	0.2139653	M209	model1	824.21593
cos_ta	-1.25924	0.477399876	-2.6377	0.008347	-2.194927	-0.3235535	M209	model1	824.21593
log_sl:cos_ta	0.3707999	0.134063805	2.765846	0.005678	0.1080397	0.6335601	M209	model1	824.21593
dist_Meadow	4.9150655	11.99796044	0.409658	0.682057	-18.6005	28.430636	M209	model2	822.3118
log_sl	-12.48175	17.40997652	-0.71693	0.473417	-46.60468	21.641176	M209	model2	822.3118
cos_ta	50.763414	41.18935203	1.23244	0.217785	-29.96623	131.49306	M209	model2	822.3118
dist_Meadow:log_sl	1.954231	2.714317966	0.719971	0.471543	-3.365734	7.2741964	M209	model2	822.3118
dist_Meadow:cos_ta	-8.121703	6.421074964	-1.26485	0.205925	-20.70678	4.4633729	M209	model2	822.3118
log_sl:cos_ta	0.3978712	0.138156028	2.879868	0.003978	0.1270903	0.668652	M209	model2	822.3118
dist_Pasture	1.9631406	2.641680467	0.743141	0.457396	-3.214458	7.1407392	M209	model3	825.61237
log_sl	0.0550268	3.539035638	0.015549	0.987595	-6.881356	6.9914092	M209	model3	825.61237
cos_ta	-6.235142	6.729643345	-0.92652	0.354176	-19.425	6.9547161	M209	model3	825.61237
dist_Pasture:log_sl	-0.001993	0.595859621	-0.00335	0.997331	-1.169857	1.1658701	M209	model3	825.61237
dist_Pasture:cos_ta	0.8319689	1.127708098	0.737752	0.460665	-1.378298	3.0422362	M209	model3	825.61237
log_sl:cos_ta	0.3853269	0.1355535	2.842619	0.004474	0.1196469	0.6510069	M209	model3	825.61237
dist_Hedge	3.0205929	2.081876797	1.450899	0.146808	-1.059811	7.1009964	M209	model4	817.8155
log_sl	-2.518291	3.274582397	-0.76904	0.441868	-8.936355	3.8997726	M209	model4	817.8155
cos_ta	0.7394111	7.869104573	0.093964	0.925138	-14.68375	16.162573	M209	model4	817.8155
dist_Hedge:log_sl	0.4390947	0.553750118	0.792947	0.427808	-0.646236	1.524425	M209	model4	817.8155
dist_Hedge:cos_ta	-0.33991	1.319555497	-0.25759	0.79672	-2.926192	2.246371	M209	model4	817.8155

log_sl:cos_ta	0.3713362	0.136547559	2.719464	0.006539	0.1037079	0.6389645	M209	model4	817.8155
dist_Woodland	0.0220464	1.8109666	0.012174	0.990287	-3.527383	3.5714757	M209	model5	829.70377
log_sl	0.3999945	2.313464499	0.172899	0.862731	-4.134313	4.9343016	M209	model5	829.70377
cos_ta	-4.515953	4.558218209	-0.99073	0.321819	-13.4499	4.4179906	M209	model5	829.70377
dist_Woodland:log_sl	-0.071689	0.434434026	-0.16502	0.868931	-0.923164	0.7797862	M209	model5	829.70377
dist_Woodland:cos_ta	0.6118841	0.851726703	0.718404	0.472508	-1.05747	2.2812378	M209	model5	829.70377
log_sl:cos_ta	0.371407	0.134695809	2.757376	0.005827	0.107408	0.6354059	M209	model5	829.70377
dist_Scrub	2.1939714	3.491951169	0.628294	0.529811	-4.650127	9.0380699	M209	model6	827.65996
log_sl	-0.765441	5.070347283	-0.15096	0.880004	-10.70314	9.1722572	M209	model6	827.65996
cos_ta	-1.761187	10.40025164	-0.16934	0.865529	-22.14531	18.622931	M209	model6	827.65996
dist_Scrub:log_sl	0.1290321	0.811921064	0.158922	0.87373	-1.462304	1.7203682	M209	model6	827.65996
dist_Scrub:cos_ta	0.0754626	1.659036512	0.045486	0.96372	-3.176189	3.3271145	M209	model6	827.65996
log_sl:cos_ta	0.3821338	0.135331417	2.823689	0.004747	0.1168891	0.6473785	M209	model6	827.65996
dist_Gardens	0.1070815	0.927285337	0.115478	0.908066	-1.710364	1.9245273	M209	model7	829.83569
log_sl	-0.028967	1.130635323	-0.02562	0.97956	-2.244972	2.1870374	M209	model7	829.83569
cos_ta	-1.999196	2.223911408	-0.89896	0.368677	-6.357983	2.3595899	M209	model7	829.83569
dist_Gardens:log_sl	0.0094387	0.226297487	0.041709	0.966731	-0.434096	0.4529736	M209	model7	829.83569
dist_Gardens:cos_ta	0.1500793	0.436611438	0.343737	0.731044	-0.705663	1.005822	M209	model7	829.83569
log_sl:cos_ta	0.3684559	0.134243867	2.744676	0.006057	0.1053428	0.6315691	M209	model7	829.83569
dist_Buildings	0.9118525	1.074473643	0.84865	0.396076	-1.194077	3.0177822	M209	model8	829.16047
log_sl	0.9223643	1.265104243	0.729082	0.465952	-1.557194	3.401923	M209	model8	829.16047
cos_ta	-2.414037	2.296683958	-1.0511	0.293214	-6.915455	2.0873805	M209	model8	829.16047
dist_Buildings:log_sl	-0.180259	0.250434079	-0.71979	0.471656	-0.671101	0.3105827	M209	model8	829.16047
dist_Buildings:cos_ta	0.2298869	0.442274491	0.519783	0.603215	-0.636955	1.096729	M209	model8	829.16047
log_sl:cos_ta	0.3718045	0.133976607	2.775145	0.005518	0.1092152	0.6343939	M209	model8	829.16047
dist_Road_Surface	0.0869912	0.786722527	0.110574	0.911954	-1.454957	1.6289391	M209	model9	830.19396
log_sl	0.1344353	0.875979425	0.153469	0.878029	-1.582453	1.8513234	M209	model9	830.19396
cos_ta	-1.416152	1.680235215	-0.84283	0.399324	-4.709352	1.8770488	M209	model9	830.19396
dist_Road_Surface:log_sl	-0.023217	0.175586689	-0.13222	0.894807	-0.36736	0.3209267	M209	model9	830.19396
dist_Road_Surface:cos_ta	0.0318062	0.324487655	0.09802	0.921917	-0.604178	0.6677903	M209	model9	830.19396

log_sl:cos_ta	0.3708319	0.134162172	2.764057	0.005709	0.1078789	0.633785	M209	model9	830.19396
log_sl	1.0103291	0.35774069	2.824194	0.00474	0.3091703	1.711488	M217	model1	163.57628
cos_ta	-6.01449	1.551249989	-3.87719	1.06E-04	-9.054884	-2.9740962	M217	model1	163.57628
log_sl:cos_ta	1.5503671	0.389770325	3.977643	6.96E-05	0.7864313	2.3143028	M217	model1	163.57628
dist_Meadow	6.3564342	14.19857512	0.447681	0.654383	-21.47226	34.18513	M217	model2	168.96563
log_sl	7.1111157	22.35958714	0.318034	0.750459	-36.71287	50.935101	M217	model2	168.96563
cos_ta	2.5886277	32.76426735	0.079008	0.937027	-61.62816	66.805412	M217	model2	168.96563
dist_Meadow:log_sl	-0.96029	3.520886607	-0.27274	0.785052	-7.8611	5.9405214	M217	model2	168.96563
dist_Meadow:cos_ta	-1.344581	5.174953685	-0.25982	0.794999	-11.4873	8.7981416	M217	model2	168.96563
log_sl:cos_ta	1.5274741	0.393604532	3.880733	1.04E-04	0.7560234	2.2989248	M217	model2	168.96563
dist_Pasture	-3.340696	2.824189278	-1.18289	0.236854	-8.876006	2.1946129	M217	model3	166.62807
log_sl	-0.82797	3.190108168	-0.25954	0.795216	-7.080467	5.4245276	M217	model3	166.62807
cos_ta	-7.13622	4.804055236	-1.48546	0.137423	-16.552	2.2795555	M217	model3	166.62807
dist_Pasture:log_sl	0.3471379	0.603732317	0.574986	0.5653	-0.836156	1.5304315	M217	model3	166.62807
dist_Pasture:cos_ta	0.2447362	0.837826076	0.292109	0.770204	-1.397373	1.8868451	M217	model3	166.62807
log_sl:cos_ta	1.4908949	0.408460742	3.650032	2.62E-04	0.6903265	2.2914632	M217	model3	166.62807
dist_Hedgerow	36.135929	24.46138499	1.477264	0.139605	-11.8075	84.079362	M217	model4	163.31591
log_sl	47.244947	36.30387989	1.301375	0.19313	-23.90935	118.39924	M217	model4	163.31591
cos_ta	29.477707	40.35825052	0.730401	0.465145	-49.62301	108.57842	M217	model4	163.31591
dist_Hedgerow:log_sl	-7.770393	6.10007128	-1.27382	0.202727	-19.72631	4.1855275	M217	model4	163.31591
dist_Hedgerow:cos_ta	-5.879522	6.77383986	-0.86797	0.385408	-19.156	7.3969602	M217	model4	163.31591
log_sl:cos_ta	1.3662238	0.425037311	3.214362	0.001307	0.533166	2.1992816	M217	model4	163.31591
dist_Woodland	-33.98886	28.76354223	-1.18166	0.237339	-90.36437	22.386648	M217	model5	165.04657
log_sl	-47.79573	41.32936422	-1.15646	0.247493	-128.7998	33.208336	M217	model5	165.04657
cos_ta	-47.06866	46.53082866	-1.01156	0.311749	-138.2674	44.130089	M217	model5	165.04657
dist_Woodland:log_sl	8.8355742	7.478400932	1.181479	0.237412	-5.821822	23.492971	M217	model5	165.04657
dist_Woodland:cos_ta	7.4656443	8.378694378	0.891027	0.372915	-8.956295	23.887583	M217	model5	165.04657
log_sl:cos_ta	1.4690025	0.426906495	3.44104	5.79E-04	0.6322811	2.3057238	M217	model5	165.04657
dist_Scrub	-6.014159	26.93987834	-0.22324	0.823346	-58.81535	46.787032	M217	model6	165.55744
log_sl	-27.57537	46.15558637	-0.59744	0.550211	-118.0387	62.887912	M217	model6	165.55744
cos_ta	-29.00484	70.72975481	-0.41008	0.681747	-167.6326	109.62293	M217	model6	165.55744

dist_Scru b:log_sl	4.5446981	7.292600394	0.623193	0.533158	-9.748536	18.837932	M217	model6	165.55744
dist_Scru b:cos_ta	3.5534449	11.13135268	0.319228	0.749553	-18.26361	25.370495	M217	model6	165.55744
log_sl:co s_ta	1.668323	0.423258962	3.941613	8.09E-05	0.8387506	2.4978953	M217	model6	165.55744
dist_Gard ens	16.714255	13.36554502	1.250548	0.211099	-9.481732	42.910242	M217	model7	161.06903
log_sl	14.582973	18.78224456	0.776423	0.437499	-22.22955	51.395496	M217	model7	161.06903
cos_ta	5.3486894	25.87184453	0.206738	0.836215	-45.35919	56.056573	M217	model7	161.06903
dist_Gard ens:log_s l	-2.522813	3.53267176	-0.71414	0.475142	-9.446722	4.4010967	M217	model7	161.06903
dist_Gard ens:cos_t a	-2.15621	4.835001679	-0.44596	0.655627	-11.63264	7.3202189	M217	model7	161.06903
log_sl:co s_ta	1.5577256	0.434065513	3.588688	3.32E-04	0.7069728	2.4084783	M217	model7	161.06903
dist_Build ings	1.668832	3.92041249	0.425678	0.670343	-6.015035	9.3526993	M217	model8	165.39959
log_sl	-1.592593	6.135222882	-0.25958	0.795186	-13.61741	10.432223	M217	model8	165.39959
cos_ta	3.4303303	9.746794342	0.351944	0.72488	-15.67304	22.533696	M217	model8	165.39959
dist_Build ings:log_ sl	0.4949344	1.160220259	0.426587	0.66968	-1.779056	2.7689243	M217	model8	165.39959
dist_Build ings:cos_ ta	-1.770936	1.849258528	-0.95765	0.338241	-5.395416	1.8535445	M217	model8	165.39959
log_sl:co s_ta	1.5444811	0.40732635	3.791754	1.50E-04	0.7461362	2.3428261	M217	model8	165.39959
dist_Roa d_Surfac e	19.389794	17.57446107	1.103294	0.2699	-15.05552	53.835105	M217	model9	163.49628
log_sl	19.253252	24.69805024	0.779545	0.435658	-29.15404	67.660541	M217	model9	163.49628
cos_ta	19.089746	31.13841427	0.613061	0.539836	-41.94042	80.119917	M217	model9	163.49628
dist_Roa d_Surfac e:log_sl	-3.281029	4.443389096	-0.73841	0.460267	-11.98991	5.4278539	M217	model9	163.49628
dist_Roa d_Surfac e:cos_ta	-4.496426	5.599034421	-0.80307	0.421933	-15.47033	6.4774796	M217	model9	163.49628
log_sl:co s_ta	1.4945603	0.407694676	3.665881	2.46E-04	0.6954934	2.2936272	M217	model9	163.49628
log_sl	0.028343	0.102870185	0.275522	0.782915	-0.173279	0.2299649	M218	model1	281.11839
cos_ta	-0.364196	0.525355378	-0.69324	0.48816	-1.393874	0.6654812	M218	model1	281.11839
log_sl:co s_ta	0.1025541	0.144621373	0.709121	0.478249	-0.180899	0.3860068	M218	model1	281.11839
dist_Mea dow	-54.84656	33.52447829	-1.63602	0.101836	-120.5533	10.860208	M218	model2	283.61458
log_sl	-78.63073	46.79151978	-1.68045	0.09287	-170.3404	13.07896	M218	model2	283.61458
cos_ta	12.43125	86.57374704	0.143591	0.885823	-157.2502	182.11268	M218	model2	283.61458
dist_Mea dow:log_ sl	12.264651	7.297241657	1.680724	0.092816	-2.03768	26.566981	M218	model2	283.61458
dist_Mea dow:cos_ ta	-1.989645	13.49672704	-0.14742	0.882803	-28.44274	24.463454	M218	model2	283.61458
log_sl:co s_ta	0.0977329	0.139799669	0.699093	0.484494	-0.176269	0.3717352	M218	model2	283.61458

dist_Pasture	4.2840941	1.718949968	2.492274	0.012693	0.915014	7.6531741	M218	model3	275.47567
log_sl	4.7198599	1.849518248	2.55194	0.010712	1.0948708	8.3448491	M218	model3	275.47567
cos_ta	8.0796239	5.014877417	1.611131	0.107151	-1.749355	17.908603	M218	model3	275.47567
dist_Pasture:log_sl	-0.804349	0.311506812	-2.58212	0.009819	-1.414891	-0.1938069	M218	model3	275.47567
dist_Pasture:cos_ta	-1.40506	0.840951481	-1.6708	0.094762	-3.053295	0.2431745	M218	model3	275.47567
log_sl:cos_ta	-0.026982	0.134913414	-0.19999	0.841485	-0.291407	0.2374436	M218	model3	275.47567
dist_Hedgerow	33.487635	14.98698614	2.234448	0.025454	4.1136824	62.861589	M218	model4	280.42653
log_sl	35.710709	15.15651669	2.356129	0.018467	6.004482	65.416936	M218	model4	280.42653
cos_ta	-32.39857	22.60117473	-1.43349	0.151718	-76.69606	11.898921	M218	model4	280.42653
dist_Hedgerow:log_sl	-5.936134	2.519445617	-2.35613	0.018467	-10.87416	-0.998111	M218	model4	280.42653
dist_Hedgerow:cos_ta	5.3155865	3.750560028	1.417278	0.156402	-2.035376	12.666549	M218	model4	280.42653
log_sl:cos_ta	0.1754816	0.147282699	1.191461	0.233473	-0.113187	0.4641504	M218	model4	280.42653
dist_Woodland	0.609854	1.72979201	0.352559	0.724419	-2.780476	4.000184	M218	model5	285.73432
log_sl	0.5170637	1.938851277	0.266686	0.789711	-3.283015	4.3171423	M218	model5	285.73432
cos_ta	5.1005365	5.23119703	0.975023	0.329549	-5.152421	15.353494	M218	model5	285.73432
dist_Woodland:log_sl	-0.091702	0.36489828	-0.25131	0.801576	-0.80689	0.6234855	M218	model5	285.73432
dist_Woodland:cos_ta	-1.029354	0.978639948	-1.05182	0.292882	-2.947453	0.8887451	M218	model5	285.73432
log_sl:cos_ta	0.1007295	0.148695363	0.677422	0.498138	-0.190708	0.3921671	M218	model5	285.73432
dist_Scrub	5.0134613	6.579453714	0.761987	0.446067	-7.882031	17.908954	M218	model6	283.60229
log_sl	-0.269581	9.055407322	-0.02977	0.97625	-18.01785	17.478691	M218	model6	283.60229
cos_ta	33.764166	25.19115733	1.340318	0.180142	-15.60959	83.137928	M218	model6	283.60229
dist_Scrub:log_sl	0.0511087	1.442619987	0.035428	0.971739	-2.776375	2.8785919	M218	model6	283.60229
dist_Scrub:cos_ta	-5.430009	4.004981431	-1.35581	0.175158	-13.27963	2.4196101	M218	model6	283.60229
log_sl:cos_ta	0.0858198	0.15387708	0.557717	0.577038	-0.215774	0.3874134	M218	model6	283.60229
dist_Gardens	3.209089	1.674671695	1.91625	0.055333	-0.073207	6.4913852	M218	model7	281.57059
log_sl	3.6665351	1.865050342	1.965918	0.049308	0.0111036	7.3219666	M218	model7	281.57059
cos_ta	2.3047382	3.603311629	0.639617	0.522422	-4.757623	9.3670992	M218	model7	281.57059
dist_Gardens:log_sl	-0.702737	0.354974458	-1.97968	0.047739	-1.398474	-0.0069999	M218	model7	281.57059
dist_Gardens:cos_ta	-0.502531	0.681511954	-0.73738	0.460893	-1.83827	0.8332076	M218	model7	281.57059
log_sl:cos_ta	0.0562971	0.141339429	0.398311	0.690401	-0.220723	0.3333173	M218	model7	281.57059

dist_Buildings	3.3460118	1.790188015	1.869084	0.061611	-0.162692	6.8547158	M218	model8	282.03011
log_sl	3.4839804	2.053163484	1.696884	0.089719	-0.540146	7.5081069	M218	model8	282.03011
cos_ta	2.8555663	4.133880724	0.690771	0.489709	-5.246691	10.957824	M218	model8	282.03011
dist_Buildings:log_sl	-0.657257	0.386292312	-1.70145	0.088858	-1.414376	0.0998616	M218	model8	282.03011
dist_Buildings:cos_ta	-0.597905	0.771794831	-0.77469	0.438521	-2.110595	0.9147855	M218	model8	282.03011
log_sl:cos_ta	0.050025	0.143337377	0.349002	0.727088	-0.230911	0.3309611	M218	model8	282.03011
dist_Road_Surface	3.0643464	1.739343683	1.761783	0.078106	-0.344705	6.4733974	M218	model9	282.62451
log_sl	3.2300097	1.960425291	1.647607	0.099433	-0.612353	7.0723727	M218	model9	282.62451
cos_ta	2.6741222	4.030477213	0.663475	0.507026	-5.225468	10.573712	M218	model9	282.62451
dist_Road_Surface:log_sl	-0.59259	0.359129982	-1.65007	0.098929	-1.296471	0.1112922	M218	model9	282.62451
dist_Road_Surface:cos_ta	-0.54812	0.731243782	-0.74957	0.453512	-1.981332	0.8850912	M218	model9	282.62451
log_sl:cos_ta	0.0524874	0.143728621	0.365184	0.714974	-0.229216	0.3341903	M218	model9	282.62451

Appendix table 3. All results from the population-level Integrated step selection analysis for Aesculapian snakes (*Zamenis longissimus*) tracked in Colwyn Bay, North Wales in 2022. Abbreviations for sl: step length, ta: turn angle.

Mean	Standard error	Lower quartile	Median Quartile	Upper Quartile	Mode	Kullback-Leibler Divergence	Term
0.021557	0.039912228	-0.06926049	0.013504944	0.088705853	0.007704	0.008465739	dist_Meadow
0.	0.000152219	-3.27E-05	0.000121816	0.000445363	6.83E-05	8.44E-07	dist_Meadow:log_sl
-0.00043	0.000495594	-0.001106821	-0.000491204	0.000780488	-0.00043	0.000231621	dist_Meadow:cos_ta
0.002661	0.005036113	-0.008748714	0.003041237	0.012208406	0.003598	0.004346846	dist_Pasture
2.49E-06	9.92E-05	-0.000192099	2.49E-06	0.000197088	2.49E-06	5.52E-11	dist_Pasture:log_sl
-0.00066	0.000195324	-0.00104389	-0.000660823	-0.000277767	-0.00066	5.53E-11	dist_Pasture:cos_ta
0.02112	0.009514358	0.001981435	0.020960951	0.040991392	0.020637	0.001995308	dist_Hedgerow
0.000158	8.97E-05	-1.76E-05	0.000158237	0.00033408	0.000158	5.60E-11	dist_Hedgerow:log_sl
-0.00065	0.000172008	-0.000991968	-0.000654632	-0.000317298	-0.00065	5.53E-11	dist_Hedgerow:cos_ta
-0.00739	0.005048417	-0.018487639	-0.007120714	0.00209396	-0.00674	0.002643693	dist_Woodland
9.81E-05	0.000174981	-0.000245071	9.81E-05	0.000441259	9.81E-05	5.53E-11	dist_Woodland:log_sl
-0.00125	0.000341452	-0.001915024	-0.001245388	-0.000575742	-0.00125	5.52E-11	dist_Woodland:cos_ta
0.008268	0.004009531	0.000343009	0.008085201	0.017234053	0.007878	0.002352335	dist_Scrub
4.83E-05	6.50E-05	-7.92E-05	4.83E-05	0.000175822	4.83E-05	5.61E-11	dist_Scrub:log_sl
-0.00049	0.000128432	-0.000739306	-0.000487408	-0.000235554	-0.00049	5.53E-11	dist_Scrub:cos_ta
0.009815	0.010351426	-0.014230498	0.010335193	0.030197763	0.010472	0.004113225	dist_Gardens
2.15E-05	0.000170709	-0.000313244	2.15E-05	0.000356327	2.15E-05	5.68E-11	dist_Gardens:log_sl
-0.0013	0.000340034	-0.001964543	-0.001297685	-0.000630825	-0.0013	5.53E-11	dist_Gardens:cos_ta
0.025503	0.012698917	0.001484987	0.024710788	0.053495223	0.023205	0.002452856	dist_Buildings
0.000105	0.000158746	-0.00020616	0.000105117	0.000416489	0.000105	5.64E-11	dist_Buildings:log_sl
-0.00128	0.000318219	-0.001900895	-0.001276818	-0.00065274	-0.00128	5.53E-11	dist_Buildings:cos_ta
0.001361	0.004585541	-0.008591983	0.00141951	0.010999971	0.001473	0.004559783	dist_Road_Surface
-7.80E-05	0.000146762	-0.00036577	-7.80E-05	0.000209875	-7.81E-05	5.76E-11	dist_Road_Surface:log_sl
-0.00107	0.000299017	-0.001657043	-0.001070619	-0.000484205	-0.00107	5.53E-11	dist_Road_Surface:cos_ta

Supplementary material

Supplementary material 1. The full script for all analyses imported from R v4.2.0 using RStudio 2022.07.1+554.

```
---
title: "Habitat selection during movement pathways in the Aesculapian
snake (Zamenis longissimus (Laurenti, 1768)) in their introduced
range in Colwyn Bay, North Wales."
author: "Jeffrey, L."
date: "2023-10-28"
output: word_document
Codes originally from Smith et al. (2020) and Muff et al. (2019)
edited Lauren Jeffrey
---

# Libraries -----
-----

library(rgdal)
library(dplyr)
library(raster)
library(readr)
library(stringr)
library(amt)
library(broom)
library(ggplot2)
library(scico)
library(ggthemes)

# Read in Data and Resources -----
-----

landuse <- readOGR("Colw.shp")

levels(landuse$R_UL_DE)

male.data1 <- read_csv(file = "male_snake_data2.csv",
  locale = locale(tz = "UTC"))

spLL <- SpatialPoints(male.data1[,c("longitude", "latitude")],
  CRS("+proj=longlat +ellps=WGS84 +datum=WGS84
+no_defs"))

spUTM30 <- spTransform(spLL, CRS("+proj=utm +zone=30 +datum=WGS84
+units=m +no_defs +ellps=WGS84 +towgs84=0,0,0"))

male.data1$x <- spUTM30@coords[,1]
male.data1$y <- spUTM30@coords[,2]

crs.proj <- CRS("+proj=utm +zone=30 +datum=WGS84 +units=m +no_defs
+ellps=WGS84 +towgs84=0,0,0")

mdat <- male.data1
```

```

mdat$datetime <- as.POSIXct(as.character(paste(mdat$date,
mdat$time)), tz = 'UTC', format="%d/%m/%Y %H:%M:%S")

# select only the information we need
mdat <- mdat %>%
  select(x = x, y = y,
         datetime = datetime, id = id)

# Function to fit iSSF model
fitted_ssf <- function(data, model){
  mod <- fit_issf(model, data = data)
  return(mod)
}

# Create Landuse Rasters -----
#do not fiddle- this
#first determines number of columns, second number of rows
(extent(landuse)[1] - extent(landuse)[2]) / 10
(extent(landuse)[3] - extent(landuse)[4]) / 10
par(mfrow=c(1,1))

##### Meadow #####
Meadow <- landuse[landuse$R_UL_DE == "Meadow",]
plot(Meadow)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Meadow.r <- rasterize(Meadow, r, field=1)
Meadow.dist.r <- distance(Meadow.r)
class(Meadow.dist.r)
# Check:
plot(Meadow.dist.r)
writeRaster(x = Meadow.dist.r, filename = "Meadow_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Meadow <- raster("Meadow_dist.tif")
dist.Meadow[] <- abs(dist.Meadow[] - max(dist.Meadow[]))
plot(dist.Meadow)
writeRaster(x = dist.Meadow, filename = "Meadow_dist_INVERT.tif",
            format = "GTiff", overwrite = TRUE)

##### Pasture #####
Pasture <- landuse[landuse$R_UL_DE == "Pasture",]
plot(Pasture)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Pasture.r <- rasterize(Pasture, r, field=1)
Pasture.dist.r <- distance(Pasture.r)
class(Pasture.dist.r)
# Check:
plot(Pasture.dist.r)
writeRaster(x = Pasture.dist.r, filename = "Pasture_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Pasture <- raster("Pasture_dist.tif")
dist.Pasture[] <- abs(dist.Pasture[] - max(dist.Pasture[]))
plot(dist.Pasture)
writeRaster(x = dist.Pasture, filename = "Pasture_dist_INVERT.tif",
            format = "GTiff", overwrite = TRUE)

```



```

##### Hedgerow #####

Hedgerow <- landuse[landuse$R_UL_DE == "Hedgerow",]
plot(Hedgerow)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Hedgerow.r <- rasterize(Hedgerow, r, field=1)
Hedgerow.dist.r <- distance(Hedgerow.r)
class(Hedgerow.r)
# Check:
plot(Hedgerow.dist.r)
writeRaster(x = Hedgerow.dist.r, filename = "Hedgerow_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Hedgerow <- raster("Hedgerow_dist.tif")
dist.Hedgerow[] <- abs(dist.Hedgerow[] - max(dist.Hedgerow[]))
plot(dist.Hedgerow)
writeRaster(x = dist.Hedgerow, filename = "Hedgerow_dist_INVERT.tif",
            format = "GTiff", overwrite = TRUE)

##### Woodland #####

Woodland <- landuse[landuse$R_UL_DE == "Woodland",]
plot(Woodland)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Woodland.r <- rasterize(Woodland, r, field=1)
Woodland.dist.r <- distance(Woodland.r)
class(Woodland.dist.r)
# Check:
plot(Woodland.dist.r)
writeRaster(x = Woodland.dist.r, filename = "Woodland_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Woodland <- raster("Woodland_dist.tif")
dist.Woodland[] <- abs(dist.Woodland[] - max(dist.Woodland[]))
plot(dist.Woodland)
writeRaster(x = dist.Woodland, filename = "Woodland_dist_INVERT.tif",
            format = "GTiff", overwrite = TRUE)

##### Scrub #####

Scrub <- landuse[landuse$R_UL_DE == "Scrub",]
plot(Scrub)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Scrub.r <- rasterize(Scrub, r, field=1)
Scrub.dist.r <- distance(Scrub.r)
class(Scrub.dist.r)
# Check:
plot(Scrub.dist.r)
writeRaster(x = Scrub.dist.r, filename = "Scrub_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Scrub <- raster("Scrub_dist.tif")
dist.Scrub[] <- abs(dist.Scrub[] - max(dist.Scrub[]))
plot(dist.Scrub)
writeRaster(x = dist.Scrub, filename = "Scrub_dist_INVERT.tif",

```

```

        format = "GTiff", overwrite = TRUE)

##### Gardens #####
Gardens <- landuse[landuse$R_UL_DE == "Park_Garden",]
plot(Gardens)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Gardens.r <- rasterize(Gardens, r, field=1)
Gardens.dist.r <- distance(Gardens.r)
class(Gardens.dist.r)
# Check:
plot(Gardens.dist.r)
writeRaster(x = Gardens.dist.r, filename = "Gardens_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Gardens <- raster("Gardens_dist.tif")
dist.Gardens[] <- abs(dist.Gardens[] - max(dist.Gardens[]))
plot(dist.Gardens)
writeRaster(x = dist.Gardens, filename = "Gardens_dist_INVERT.tif",
            format = "GTiff", overwrite = TRUE)

##### Buildings #####
Buildings <- landuse[landuse$R_UL_DE == "Building",]
plot(Buildings)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Buildings.r <- rasterize(Buildings, r, field=1)
Buildings.dist.r <- distance(Buildings.r)
class(Buildings.dist.r)
# Check:
plot(Buildings.dist.r)
writeRaster(x = Buildings.dist.r, filename = "Buildings_dist.tif",
            format = "GTiff", overwrite = TRUE)
dist.Buildings <- raster("Buildings_dist.tif")
dist.Buildings[] <- abs(dist.Buildings[] - max(dist.Buildings[]))
plot(dist.Buildings)
writeRaster(x = dist.Buildings, filename =
"Buildings_dist_INVERT.tif",
            format = "GTiff", overwrite = TRUE)

##### Road Surface #####
## putting roads and bare_ground areas together in raster
Road_Surface <- landuse[landuse$R_UL_DE == "Roads" |
                        landuse$R_UL_DE == "Bare_Ground",]

plot(Road_Surface)
r <- raster(x = extent(landuse), nrows = 120, ncols = 147)
proj4string(r) <- CRS(proj4string(landuse))
r[] <- NA
Road_Surface.r <- rasterize(Road_Surface, r, field=1)
Road_Surface.dist.r <- distance(Road_Surface.r)
class(Road_Surface.dist.r)
# Check:
plot(Road_Surface.dist.r)
writeRaster(x = Road_Surface.dist.r, filename =
"Road_Surface_dist.tif",
            format = "GTiff", overwrite = TRUE)

```

```

dist.Road_Surface <- raster("Road_Surface_dist.tif")
dist.Road_Surface[] <- abs(dist.Road_Surface[] -
max(dist.Road_Surface[]))
plot(dist.Road_Surface)
writeRaster(x = dist.Road_Surface, filename =
"Road_Surface_dist_INVERT.tif",
          format = "GTiff", overwrite = TRUE)

# Read Habitat Raster and Set SSF Parameters -----
-----

list.files()
covariates <- list("Meadow_dist_INVERT.tif",
                  "Pasture_dist_INVERT.tif",
                  "Hedgerow_dist_INVERT.tif",
                  "Woodland_dist_INVERT.tif",
                  "Scrub_dist_INVERT.tif",
                  "Gardens_dist_INVERT.tif",
                  "Buildings_dist_INVERT.tif",
                  "Road_Surface_dist_INVERT.tif")

rp <- stack(x = covariates)

cov.names <- c("dist_Meadow", "dist_Pasture", "dist_Hedgerow",
              "dist_Woodland", "dist_Scrub", "dist_Gardens", "dist_Buildings",
              "dist_Road_Surface")

names(rp) <- cov.names

## Plot the variables to check they are all present
plot(rp)

## Testing for correlation between raster data sets
# Overall correlation between variables
globalCor <- cor(values(rp),
                 values(rp))
globalCor

# Run again if you are doing playing with values in the loop
all.ssfResults <- NULL
ind.ssfResults <- NULL
# rm(data.1, ssf1, tr1)

# Specify the snakes to use
# snake_ids <- c("M031", "M074", "M154", "M202", "M209", "M217",
               "M218")

# Use only those snakes that used a variety of habitats
snake_ids <- c("M031", "M154", "M202", "M209", "M217", "M218")

## Create model sets to run for the iSSF analysis
mods <- list()

# single factor models
mods[[1]] <- case_ ~ log_sl * cos_ta + strata(step_id_)
mods[[2]] <- case_ ~ dist_Meadow + dist_Meadow:log_sl +
dist_Meadow:cos_ta +
log_sl * cos_ta + strata(step_id_)

```

```

mods[[3]] <- case_ ~ dist_Pasture + dist_Pasture:log_sl +
  dist_Pasture:cos_ta +
  log_sl * cos_ta + strata(step_id_)
mods[[4]] <- case_ ~ dist_Hedgerow + dist_Hedgerow:log_sl +
  dist_Hedgerow:cos_ta +
  log_sl * cos_ta + strata(step_id_)
mods[[5]] <- case_ ~ dist_Woodland + dist_Woodland:log_sl +
  dist_Woodland:cos_ta +
  log_sl * cos_ta + strata(step_id_)
mods[[6]] <- case_ ~ dist_Scrub + dist_Scrub:log_sl +
  dist_Scrub:cos_ta +
  log_sl * cos_ta + strata(step_id_)
mods[[7]] <- case_ ~ dist_Gardens + dist_Gardens:log_sl +
  dist_Gardens:cos_ta +
  log_sl * cos_ta + strata(step_id_)
mods[[8]] <- case_ ~ dist_Buildings + dist_Buildings:log_sl +
  dist_Buildings:cos_ta +
  log_sl * cos_ta + strata(step_id_)
mods[[9]] <- case_ ~ dist_Road_Surface + dist_Road_Surface:log_sl +
  dist_Road_Surface:cos_ta +
  log_sl * cos_ta + strata(step_id_)

# SSF Loop per Individual -----
-----

i <- 0
ssfResults <- vector(mode = "list", length = length(snake_ids))
for(snake in snake_ids){
  i <- i+1
  # snake <- "M031"
  data.1 <- dplyr::filter(mdat, id == snake)
  # data.1 <-dplyr::filter(data.1, datetime >'2022-07-01 00:00:00' )
  #checking the breeding season
  # data.1 <-dplyr::filter(data.1, datetime <'2022-08-01 00:00:00' )
  #checking the non-breeding season

  # Uncomment to test loop
  #data.1 <- dplyr::filter(male.data1, id == 'M031')

  # Creates the track data using package 'amt'
  tr1 <- mk_track(data.1, x, y, datetime, crs = crs.proj, id = id)
  tr1 <- track_resample(tr1, rate = hours (2), tolerance = hours (4))

  # Calculates step and angle variables,
  ssf1 <- tr1 %>%
  # filter_min_n_burst(min_n =3) %>% ## selecting steps during
  bursts only - no overnights
  steps() %>%
  filter(sl_ > 0) # filter small movements
  # %>%
  # # Extracts whether each point originated in the protected area
  and removes them
  # extract_covariates(pro.area, where = "start") %>%
  # filter(protected == 1)

  # Create random steps and extract covariates
  ssf1 <- ssf1 %>%
  random_steps(n = 200) %>%

```

```

extract_covariates(rp, where = "end")

# Creates the transformed variables used in the models
ssf1 <- ssf1 %>%
  mutate(dist_Meadow = log(dist_Meadow),
         dist_Pasture = log(dist_Pasture),
         dist_Hedgerow = log(dist_Hedgerow),
         dist_Woodland = log(dist_Woodland),
         dist_Scrub = log(dist_Scrub),
         dist_Gardens = log(dist_Gardens),
         dist_Buildings = log(dist_Buildings),
         dist_Road_Surface = log(dist_Road_Surface),
         cos_ta = cos(ta_),
         log_sl = log(sl_))

ssf1 <- ssf1[!is.infinite(ssf1$dist_Road_Surface),] # remove
infinite values
ssf1 <- ssf1[!is.infinite(ssf1$dist_Gardens),] # remove infinite
values
ssf1 <- ssf1[!is.infinite(ssf1$dist_Buildings),] # remove infinite
values
ssf1 <- ssf1[!is.infinite(ssf1$dist_Woodland),] # remove infinite
values
ssf1 <- ssf1[!is.infinite(ssf1$dist_Scrub),] # remove infinite
values
# Set the individual ID for the current data set
ssf1$id <- snake

?fit_issf()

# Runs a loop and fits an iSSF for all model sets
ind.ssfResults <- NULL
iter <- 0
for(model in mods){
  iter <- iter + 1
  ssffit <- fit_issf(ssf1, formula = model)
  results_ssf <- tidy(ssffit$model, conf.int = TRUE)
  results_ssf$id <- snake
  results_ssf$model <- paste0('model',iter)
  results_ssf$AIC <- AIC(ssffit$model)
  ind.ssfResults <- rbind(ind.ssfResults, results_ssf)
}
ssfResults[[i]] <- ind.ssfResults
} # end of indi loop

# Review Results -----
-----

all.ssfResults <- do.call(rbind, ssfResults)
write_csv(all.ssfResults, "All_ssf_results.csv")

# Create AIC table for all individuals
ssf.AIC.results <- all.ssfResults %>%
  group_by(model, id) %>%
  summarise(AIC = mean(AIC)) %>%
  arrange(AIC)

```

```

ssf.AIC.results
write_csv(ssf.AIC.results, "ssfAIC_results.csv")

ssf.AIC.results.t2 <- ssf.AIC.results %>%
  group_by(id) %>%
  mutate(AIC = ifelse(AIC < min(AIC)+2, paste0("*",
                                                    round(AIC, digits =
2),
                                                    "*"),
                    round(AIC, digits = 2))) %>%
  mutate(model = factor(model, levels = c("model1", "model2",
"model3", "model4", "model5", "model6", "model7", "model8",
"model9"))) %>%
  arrange(model)

# ssf.AIC.results.t2$AIC <- round(ssf.AIC.results$AIC)
table.2 <- reshape2::dcast(ssf.AIC.results.t2, model ~ id)
table.2

write_csv(table.2, "AIC scores and models.csv")

table.2$formula <-
  c("log_sl*cos_ta+strata(step_id_)",
    "log_sl*cos_ta+strata(step_id_)+dist_Meadow+dist_Meadow:log_sl+dist_M
eadow:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Pasture+dist_Pasture:log_sl+dist
_Pasture:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Hedgerow+dist_Hedgerow:log_sl+di
st_Hedgerow:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Woodland+dist_Woodland:log_sl+di
st_Woodland:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Scrub+dist_Scrub:log_sl+dist_Scr
ub:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Gardens+dist_Gardens:log_sl+dist
_Gardens:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Buildings+dist_Buildings:log_sl+
dist_Buildings:cos_ta",
    "log_sl*cos_ta+strata(step_id_)+dist_Road_Surface+dist_Road_Surface:l
og_sl+dist_Road_Surface:cos_ta")

table.2 <- table.2 %>%
  dplyr::select(model, formula, contains("0")) %>%
  rename("Model #" = model,
        "Model formula" = formula)

# Return the top model for each individual
top.models <- ssf.AIC.results %>%
  group_by(id) %>%
  filter(AIC == min(AIC)) %>%
  arrange(model)

```

```

top.models

topmodelsdf <- as.data.frame(top.models)

write_csv(top.models, "ssf_AICresults_topmodels.csv")

##### Making figures for individual level ISSF
ssf.results <- read.csv(file = "All_ssf_results.csv",
stringsAsFactors = FALSE)

### dist_feature plot
ssf.results %>%
  group_by(id) %>%
  mutate(best = ifelse(AIC <= min(AIC)+2, "*", "")) %>%
  filter(term %in% grep("log_sl|cos_ta", term, value = TRUE,
invert = TRUE)) %>%

  group_by(id) %>%
  #mutate(term = factor(term, levels = c("Meadow", "Pasture", "Road",
"Ba.Ga.", "Buildings", "Hedgerow",
#"Gardens", "Scrub", "Woodland"))) %>%
  arrange(term) %>%
  mutate(plot.order = row_number()) %>%
  ggplot() +
  geom_hline(aes(yintercept = 0), linetype = 2, alpha = 0.5) +
  geom_errorbar(aes(x = plot.order, ymin = conf.low, ymax =
conf.high,
                    colour = term),
                width = 0.25) +
  geom_point(aes(x = plot.order, y = estimate, colour = term,
shape = best)) +
  facet_wrap(~id) +
  scale_shape_manual(values = c(3, 16)) +
  scale_x_continuous(labels = c(),
                    breaks = c(1.5, 3.5, 6, 9, 11.5, 14, 17, 20),
                    minor_breaks = c(2.5, 4.5, 7.5, 10.5, 12.5,
14.5, 16.5, 18.5)
) +
  coord_cartesian(ylim = c(-40, 40)) +
  labs(x = "Feature", y = expression(beta), colour = "Distance
to\nfeature:") +
  scale_colour_manual(values = c("#D55E00",
"#E69F00",
"#0072B2",
"#009E73",
"#F0E442",
"#56B4E9",
"#CC79A7",
"#999999"),
                    labels = c("Meadow",
"Pasture",
"Hedgerow",
"Woodland",
"Scrub",
"Gardens",
"Buildings",
"Road Surface")) +

  theme_bw() +

```

```

theme(axis.text.x = element_text(angle = 0, hjust = 0.5, vjust =
0.5),
      strip.background = element_blank(),
      strip.text = element_text(face = 4, hjust = 0),
      panel.grid.major.x = element_blank(),
      panel.grid.minor.x = element_line(colour = "grey65", linetype
= 1),
      panel.grid.minor.y = element_blank(),
      legend.position = "bottom",
      legend.title = element_text(face = 2),
      legend.text = element_text(lineheight = 1),
      legend.background = element_blank(),
      axis.title.y = element_text(angle = 0, vjust = 1, face = 2),
      axis.title.x = element_text(hjust = 0.5, face = 2, margin =
margin(10,0,0,0)),
      plot.title = element_text(face = 4),
      strip.text.y = element_blank()
) +
guides(shape = guide_none())

ggsave(file = "SSF all model results.png", width = 200, height = 150,
        dpi = 300, units = "mm")

#### step length interaction plot
ssf.results %>%
  group_by(id) %>%
  mutate(best = ifelse(AIC <= min(AIC)+2, "*", "")) %>%
  filter(term %in% grep("log_sl", term, value = TRUE,
                        invert = FALSE)) %>%
  filter(!term %in% c("log_sl:cos_ta", "log_sl", "cos_ta")) %>%
  mutate(term = str_to_title(sub("dist_", "", term)),
         term = ifelse(term == "Hedgerow", "Gardens", term),
         best.model = ifelse( (model == 'model3' & id %in%
c("M218")) |
                                (model == 'model4' & id %in%
c("M154", "209")) |
                                (model == 'model7' & id %in%
c("M217")) |
                                (model == 'model8' & id %in%
c("M031", "M202")),
         "*", "")) %>%
  mutate(term = factor(term, levels = c("Log_sl:cos_ta",
                                        "Meadow:log_sl",
                                        "Pasture:log_sl",
                                        "Hedgerow:log_sl",
                                        "Woodland:log_sl",
                                        "Scrub:log_sl",
                                        "Gardens:log_sl",
                                        "Buildings:log_sl",
                                        "Road_Surface:log_sl",
                                        "Meadow:cos_ta",
                                        "Pasture:cos_ta",
                                        "Hedgerow:cos_ta",
                                        "Woodland:cos_ta",
                                        "Scrub:cos_ta",
                                        "Gardens:cos_ta",
                                        "Buildings:cos_ta",
                                        "Road_Surface:cos_ta"

```



```

))) %>%
  arrange(term) %>%
  ggplot() +
  geom_hline(aes(yintercept = 0), linetype = 2, alpha = 0.5) +
  geom_errorbar(aes(x = term, ymin = conf.low, ymax = conf.high,
                    colour = term),
                width = 0.25) +
  geom_point(aes(x = term, y = estimate, colour = term)) +
  facet_wrap(~id, scales = "free_y") +
  scale_shape_manual(values = c(3, 16)) +
  scale_x_discrete(labels = c()) +
  # coord_cartesian(ylim = c(-250, 250)) +
  labs(x = "Feature", y = expression(beta), colour = "Step
length\ninteraction with:") +
  scale_colour_manual(values = c("#D55E00",
                                  "#E69F00",
                                  "#0072B2",
                                  "#009E73",
                                  "#F0E442",
                                  "#56B4E9",
                                  "#CC79A7",
                                  "#999999"),
                      labels = c("Meadow",
                                  "Pasture",
                                  "Hedgerow",
                                  "Woodland",
                                  "Scrub",
                                  "Gardens",
                                  "Buildings",
                                  "Road Surface")) +

  theme_bw() +
  theme(axis.text.x = element_text(angle = 0, hjust = 0.5, vjust =
0.5),
        strip.background = element_blank(),
        strip.text = element_text(face = 4, hjust = 0),
        panel.grid.major.x = element_blank(),
        panel.grid.minor.x = element_line(colour = "grey65", linetype
= 1),
        panel.grid.minor.y = element_blank(),
        legend.position = "bottom",
        legend.title = element_text(face = 2),
        legend.text = element_text(lineheight = 1),
        legend.background = element_blank(),
        axis.title.y = element_text(angle = 0, vjust = 1, face = 2),
        axis.title.x = element_text(hjust = 0.5, face = 2, margin =
margin(10,0,0,0)),
        plot.title = element_text(face = 4),
        strip.text.y = element_blank()
  ) +
  guides(shape = guide_none())

ggsave(file = "SSF step length interaction.png", width = 200, height
= 150,
        dpi = 300, units = "mm")

library(dplyr)
library(raster)
library(amt)

```

```

library(ggplot2)
#install.packages("INLA", repos=c(getOption("repos"),
#                                INLA="https://inla.r-inla-
download.org/R/stable"), dep=TRUE)
library(INLA)
inla.setOption(inla.mode="experimental")
library(viridis)
library(sp)

# Read in animal tracking data -----

# Males only

male.data <- read.csv(file = "male_snake_data.csv", stringsAsFactors
= FALSE)

spLL <- SpatialPoints(data[,c("latitude", "longitude")],
                      CRS("+proj=longlat +ellps=WGS84 +datum=WGS84
+no_defs"))

spUTM30 <- spTransform(spLL, CRS("+proj=utm +zone=30 +datum=WGS84
+units=m +no_defs +ellps=WGS84 +towgs84=0,0,0"))

data$x <- spUTM30@coords[,1]
data$y <- spUTM30@coords[,2]

crs.proj <- CRS("+proj=utm +zone=30 +datum=WGS84 +units=m +no_defs
+ellps=WGS84 +towgs84=0,0,0")

mdat <- male.data

mdat$datetime <- as.POSIXct(as.character(paste(mdat$date,
mdat$time)), tz = 'UTC', format="%d/%m/%Y %H:%M:%S")

# select only the information we need
mdat <- mdat %>%
  select(x = x, y = y,
         t = datetime, id = id)

# Check each individual for outliers using a gradient of colour from
# point 1 to last point -Purple/Blue to Yellow, change the name of
# the individual to check each one

##M217 <- subset(mdat, id == "M217")

#plot(M217$x, M217$y, col = viridis_pal()(nrow(M217)), pch= 20,
#      xlab = "x", ylab= "y", asp = 1)

#M217 %>%
# ggplot() +
#geom_path(aes(x = M217$x, y = M217$y, colour = t)) +
#geom_point(aes(x = M217$x, y = M217$y, colour = t)) +
#coord_equal() +
#labs(title = "M217 Movement Pathway") +
#xlab("Easting") +
#ylab("Northing")

# Load in raster covariates -----

```

```

## reading inverted tifs from ISSF code
covariates <- list("Meadow_dist_INVERT.tif",
                  "Pasture_dist_INVERT.tif",
                  "Hedgerow_dist_INVERT.tif",
                  "Woodland_dist_INVERT.tif",
                  "Scrub_dist_INVERT.tif",
                  "Gardens_dist_INVERT.tif",
                  "Buildings_dist_INVERT.tif",
                  "Road_Surface_dist_INVERT.tif")

rp <- stack(x = covariates)

cov.names <- c("dist_Meadow", "dist_Pasture", "dist_Hedgerow",
              "dist_Woodland", "dist_Scrub",
              "dist_Gardens", "dist_Buildings", "dist_Road_Surface")

names(rp) <- cov.names

## Filter out snakes with poor quality data eg short tracking
duration

#mdat <- subset(mdat, id %in% c("M154", "M202", "M209", "M218"))
mdat <- subset(mdat, id %in% c("M031", "M154", "M202", "M209",
                              "M217", "M218"))
#mdat <- subset(mdat, id %in% c("M154", "M202", "M209", "M218"))

# Filter certain dates
# mdat <- subset(mdat, t < '2022-07-01 00:00:00')

# START OF IMPORTED (and edited) CODE from Muff et al -----
-----

# separate the individuals out into a list-column of dataframes, each
item an animal
mdat_all <- mdat %>%
  nest(data = -id)
# if you want to add meta data, like sex, do so here. We had a second
dataframe
# that included metadata
#mdat_all <- left_join(mdat_all,
#                      snake.meta %>%
#                      select(id = deployment.id, sex = animal.sex))
# map operates a lot like an apply or loop. It repeats the function
to each item
# in the list. In this case we make all the individual dataframes
into track
# objects. Check dat_all to see the list of dataframes now has a
second
# dataframe/tibble for the track.
# track_resample removes overnight gaps
mdat_all <- mdat_all %>%
  mutate(trk = map(data, function(d) {
    make_track(d, x, y, t, crs = crs.proj) %>% track_resample(rate =
hours (2), tolerance = hours (4))
  })))

```

```

# Here the summarize_sampling_rate is repeated on each track object
to give you
# an individual level summary.
mdat_all %>%
  mutate(sr = lapply(trk, summarize_sampling_rate)) %>%
  select(id, sr) %>%
  unnest(cols = c(sr))

# So dat_all is set up ready for the generation of random steps and
the
# extraction of raster covariate values

# Step-Selection function -----
-----

# To make the random steps we use the map function again to do this
on an
# individual basis. We calculate the step lengths so we have data to
draw from
# to generate the random locations. Then we drop out the zero step
lengths that
# break things, or we can drop the sub-GPS error points because we
cannot be
# confident they were moves (ie not a new selection choice from the
animal).
# Then the random steps, can be generous here because we aren't using
GPS data
# with the high resolution that often entails. We have use more
randoms to pick
# up smaller changes and maximise the high res rasters we have. Final
step is to
# get the covariate values. After the mutate+map bit is a few lines
to compile
# the data into a single v large dataframe for the model.
mdat_ssf <- mdat_all %>%
  mutate(stps = map(trk, ~ .x %>%
                    steps() %>%
                    filter(sl_>0) %>% # removing the non-moves, or
under GPS error
                    random_steps(n = 200) %>%
                    extract_covariates(rp))) %>%

  select(id, stps) %>%
  unnest(cols = c(stps)) %>%
  mutate(
    y = as.numeric(case_),
    id = as.numeric(factor(id)),
    step_id = paste0(id, step_id_, sep = "-"),
    cos_ta = cos(ta_),
    log_sl = log(sl_))

# So dat_ssf is the correct format for the modelling. We have the id,
# movement columns, and the critical case_ that describes whether
they used a
# location or not.

# Running the INLA model -----
-----

```

```

# We can run the INLA model using the priors and set-up from Muff et
al.
# Precision for the priors of slope coefficients
prec.beta.trls <- 1e-4

# "In the model formula for INLA, we set the stratum-specific
intercept variance
# to  $10^6$  (or rather: the precision to  $10^{-6}$ ) by fixing
it (`fixed=T`)
# to an initial value. The other precision is given a PC(1,0.05)
prior:"

##### For Snake data
### making formulas for each habitat feature

# Meadows
formula.random.Mm <- y ~ -1 +
  dist_Meadow + # fixed covariate effect
  dist_Meadow:log_sl + # covar interactions
  dist_Meadow:cos_ta +
  f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
  f(id, dist_Meadow, values = 1:length(unique(mdat_ssf$id)),
model="iid",
  hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Pasture
formula.random.Pm <- y ~ -1 +
  dist_Pasture + # fixed covariate effect
  dist_Pasture:log_sl + # covar interactions
  dist_Pasture:cos_ta +
  f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
  f(id, dist_Pasture, values = 1:length(unique(mdat_ssf$id)),
model="iid",
  hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Hedgerows
formula.random.Hm <- y ~ -1 +
  dist_Hedgerow + # fixed covariate effect
  dist_Hedgerow:log_sl + # covar interactions
  dist_Hedgerow:cos_ta +
  f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
  f(id, dist_Hedgerow, values = 1:length(unique(mdat_ssf$id)),
model="iid",
  hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Woodland
formula.random.Wm <- y ~ -1 +
  dist_Woodland + # fixed covariate effect
  dist_Woodland:log_sl + # covar interactions

```

```

    dist_Woodland:cos_ta +
    f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
    f(id, dist_Woodland, values = 1:length(unique(mdat_ssf$id)),
model="iid",
    hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Scrub
formula.random.Sm <- y ~ -1 +
    dist_Scrub + # fixed covariate effect
    dist_Scrub:log_sl + # covar interactions
    dist_Scrub:cos_ta +
    f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
    f(id, dist_Scrub, values = 1:length(unique(mdat_ssf$id)),
model="iid",
    hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Parks and Gardens
formula.random.PGm <- y ~ -1 +
    dist_Gardens + # fixed covariate effect
    dist_Gardens:log_sl + # covar interactions
    dist_Gardens:cos_ta +
    f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
    f(id, dist_Gardens, values = 1:length(unique(mdat_ssf$id)),
model="iid",
    hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Buildings
formula.random.BUm <- y ~ -1 +
    dist_Buildings + # fixed covariate effect
    dist_Buildings:log_sl + # covar interactions
    dist_Buildings:cos_ta +
    f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
    f(id, dist_Buildings, values = 1:length(unique(mdat_ssf$id)),
model="iid",
    hyper = list(theta = list(initial = log(1), fixed = FALSE,
prior = "pc.prec", param = c(1,
0.05))))

# Road_Surface
formula.random.Rm <- y ~ -1 +
    dist_Road_Surface + # fixed covariate effect
    dist_Road_Surface:log_sl + # covar interactions
    dist_Road_Surface:cos_ta +
    f(step_id, model="iid", hyper = list(theta = list(initial = log(1e-
6), fixed = TRUE))) +
    f(id, dist_Road_Surface, values = 1:length(unique(mdat_ssf$id)),
model="iid",
    hyper = list(theta = list(initial = log(1), fixed = FALSE,

```

```

                                prior = "pc.prec", param = c(1,
0.05))))

# Last two parts of the model are the gaussian processes to deal with
step_id
# (each move), and the id of the animal. So steps_id is the
covariate, then in
# the second one is id that is weighted by the raster cov.

# Fit the models -----
-----

# Meadows
inla.ssf.Mm <- inla(formula.random.Mm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

# Pasture
inla.ssf.Pm <- inla(formula.random.Pm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

# Hedgerows
inla.ssf.Hm <- inla(formula.random.Hm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

# Woodland
inla.ssf.Wm <- inla(formula.random.Wm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

# Scrub
inla.ssf.Sm <- inla(formula.random.Sm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

# Parks and Gardens
inla.ssf.PGm <- inla(formula.random.PGm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

```

```

)
# Buildings
inla.ssf.BUm <- inla(formula.random.BUm, family = "Poisson", data =
mdat_ssf,
                    control.fixed = list(
                      mean = 0,
                      prec = list(default = prec.beta.trls))
)

# Road_Surface
inla.ssf.Rm <- inla(formula.random.Rm, family = "Poisson", data =
mdat_ssf,
                   control.fixed = list(
                     mean = 0,
                     prec = list(default = prec.beta.trls))
)

# Model results -----
-----

# We can see a dataframe of the fixed effects here, so each covar and
any interaction terms
inla.ssf.Mm$summary.fixed
inla.ssf.Pm$summary.fixed
inla.ssf.Hm$summary.fixed
inla.ssf.Wm$summary.fixed
inla.ssf.Sm$summary.fixed
inla.ssf.PGm$summary.fixed
inla.ssf.BUm$summary.fixed
inla.ssf.Rm$summary.fixed

# "Since variances are parameterized and treated as precisions, the
summary of
# the respective posterior distributions is given for the
precisions:"

inla.ssf.Mm$summary.hyperpar
inla.ssf.Pm$summary.hyperpar
inla.ssf.Hm$summary.hyperpar
inla.ssf.Wm$summary.hyperpar
inla.ssf.Sm$summary.hyperpar
inla.ssf.PGm$summary.hyperpar
inla.ssf.BUm$summary.hyperpar
inla.ssf.Rm$summary.hyperpar

inla_mmarginal <- function(r.out){
  results <- sapply(r.out$marginals.hyperpar,
                    function(y)
                      inla.mmarginal(inla.tmarginl(function(x) 1/x,
y)))

  names(results) <- sapply(as.vector(as.character(names(results))),
function(y) gsub("Precision", x=y, "Mode of variance"))
  results
}
inla_emarginal <- function(r.out){
  results <- sapply(r.out$marginals.hyperpar,

```



```

function(y)
  inla.emarginal(function(x) x,
inla.tmarginal(function(x) 1/x, y))

  names(results) <- sapply(as.vector(as.character(names(results))),
function(y) gsub("Precision", x=y, "Mean of variance"))
  results
}

# "Posterior mean and mode are obtained as"
inla_emarginal(inla.ssf.Mm)
inla_mmarginal(inla.ssf.Mm)

inla_emarginal(inla.ssf.Pm)
inla_mmarginal(inla.ssf.Pm)

inla_emarginal(inla.ssf.Hm)
inla_mmarginal(inla.ssf.Hm)

inla_emarginal(inla.ssf.Wm)
inla_mmarginal(inla.ssf.Wm)

inla_emarginal(inla.ssf.Sm)
inla_mmarginal(inla.ssf.Sm)

inla_emarginal(inla.ssf.PGm)
inla_mmarginal(inla.ssf.PGm)

inla_emarginal(inla.ssf.BUm)
inla_mmarginal(inla.ssf.BUm)

inla_emarginal(inla.ssf.Rm)
inla_mmarginal(inla.ssf.Rm)

fixed.df.Mm <- inla.ssf.Mm$summary.fixed
fixed.df.Pm <- inla.ssf.Pm$summary.fixed
fixed.df.Hm <- inla.ssf.Hm$summary.fixed
fixed.df.Wm <- inla.ssf.Wm$summary.fixed
fixed.df.Sm <- inla.ssf.Sm$summary.fixed
fixed.df.PGm <- inla.ssf.PGm$summary.fixed
fixed.df.BUm <- inla.ssf.BUm$summary.fixed
fixed.df.Rm <- inla.ssf.Rm$summary.fixed

fixed.df.Mm <- inla.ssf.Mm$summary.fixed
fixed.df.Mm$term <- row.names(fixed.df.Mm)
names(fixed.df.Mm) <- c("mean", "sd", "q025", "q50", "q975",
"mode", "kld", "term")

fixed.df.Pm <- inla.ssf.Pm$summary.fixed
fixed.df.Pm$term <- row.names(fixed.df.Pm)
names(fixed.df.Pm) <- c("mean", "sd", "q025", "q50", "q975",
"mode", "kld", "term")

fixed.df.Hm <- inla.ssf.Hm$summary.fixed
fixed.df.Hm$term <- row.names(fixed.df.Hm)
names(fixed.df.Hm) <- c("mean", "sd", "q025", "q50", "q975",
"mode", "kld", "term")

```

```

fixed.df.Wm <- inla.ssf.Wm$summary.fixed
fixed.df.Wm$term <- row.names(fixed.df.Wm)
names(fixed.df.Wm) <- c("mean", "sd", "q025", "q50", "q975",
                        "mode", "kld", "term")

fixed.df.Sm <- inla.ssf.Sm$summary.fixed
fixed.df.Sm$term <- row.names(fixed.df.Sm)
names(fixed.df.Sm) <- c("mean", "sd", "q025", "q50", "q975",
                        "mode", "kld", "term")

fixed.df.PGm <- inla.ssf.PGm$summary.fixed
fixed.df.PGm$term <- row.names(fixed.df.PGm)
names(fixed.df.PGm) <- c("mean", "sd", "q025", "q50", "q975",
                        "mode", "kld", "term")

fixed.df.BUm <- inla.ssf.BUm$summary.fixed
fixed.df.BUm$term <- row.names(fixed.df.BUm)
names(fixed.df.BUm) <- c("mean", "sd", "q025", "q50", "q975",
                        "mode", "kld", "term")

fixed.df.Rm <- inla.ssf.Rm$summary.fixed
fixed.df.Rm$term <- row.names(fixed.df.Rm)
names(fixed.df.Rm) <- c("mean", "sd", "q025", "q50", "q975",
                        "mode", "kld", "term")

allmodsm <- rbind(fixed.df.Mm, fixed.df.Pm, fixed.df.Hm,
                 fixed.df.Wm, fixed.df.Sm, fixed.df.PGm,
                 fixed.df.BUm, fixed.df.Rm)

write.csv(allmodsm, "Pop_ssf_mods_males.csv")

##### figures for population level ssf
popssfm <- read.csv(file = "Pop_ssf_mods_males.csv")

#### Distance_feature plot

popssfm %>%
  filter(term %in% grep("log_sl|cos_ta", term, value = TRUE,
                      invert = TRUE)) %>%
  mutate(term = factor(term, levels = c("dist_Meadow",
"dist_Pasture", "dist_Hedgerow", "dist_Woodland",
"dist_Scrub", "dist_Gardens",
"dist_Buildings", "dist_Road_Surface"))) %>%
  arrange(term) %>%
  ggplot() +
  geom_hline(aes(yintercept = 0), linetype = 2, alpha = 0.5) +
  geom_point(aes(x = term, y = mean, colour = term)) +
  geom_errorbar(aes(x = term, ymin = q025, ymax = q975,
                   colour = term),
               width = 0.25) +
  #facet_wrap(~id) +
  scale_shape_manual(values = c(3, 16)) +
  scale_x_discrete(labels = c()
) +
  labs(x = "Feature", y = expression(beta), colour = "Distance
to\nfeature:") +
  scale_colour_manual(values = c("#D55E00",

```

```

        "#E69F00",
        "#0072B2",
        "#009E73",
        "#F0E442",
        "#56B4E9",
        "#CC79A7",
        "#999999"),
    labels = c("Meadow",
              "Pasture",
              "Hedgerow",
              "Woodland",
              "Scrub",
              "Gardens",
              "Buildings",
              "Road_Surface")) +
  theme_bw() +
  theme(axis.text.x = element_text(angle = 0, hjust = 0.5, vjust =
0.5),
        strip.background = element_blank(),
        strip.text = element_text(face = 4, hjust = 0),
        panel.grid.major.x = element_blank(),
        panel.grid.minor.x = element_line(colour = "grey65", linetype
= 1),
        panel.grid.minor.y = element_blank(),
        legend.position = "bottom",
        legend.title = element_text(face = 2),
        legend.text = element_text(lineheight = 1),
        legend.background = element_blank(),
        axis.title.y = element_text(angle = 0, vjust = 1, face = 2),
        axis.title.x = element_text(hjust = 0.5, face = 2, margin =
margin(10,0,0,0)),
        plot.title = element_text(face = 4),
        strip.text.y = element_blank()
) +
  guides(shape = guide_none())

ggsave(file = "SSF distance to features males.png", width = 200,
height = 150,
        dpi = 300, units = "mm")

### interaction between step length and feature plot

popssfm %>%
  filter(term %in% grep("log_sl", term, value = TRUE,
invert = FALSE)) %>%
  arrange(term) %>%
  ggplot() +
  geom_hline(aes(yintercept = 0), linetype = 2, alpha = 0.5) +
  geom_errorbar(aes(x = term, ymin = q025, ymax = q975,
                    colour = term),
                width = 0.25) +
  geom_point(aes(x = term, y = mean, colour = term)) +
  #facet_wrap(~id, scales = "free_y") +
  #scale_shape_manual(values = c(3, 16)) +
  scale_x_discrete(labels = c()) +
  labs(x = "Feature", y = expression(beta), colour = "Step
length\ninteraction with:") +
  scale_colour_manual(values = c( "#D55E00",

```

```

                                "#E69F00",
                                "#0072B2",
                                "#009E73",
                                "#F0E442",
                                "#56B4E9",
                                "#CC79A7",
                                "#999999"),
                                labels = c("Meadow", "Pasture", "Hedgerow",
"Woodland",
                                "Scrub", "Gardens",
"Buildings", "Road_Surface")) +
  theme_bw() +
  theme(axis.text.x = element_text(angle = 0, hjust = 0.5, vjust =
0.5),
        strip.background = element_blank(),
        strip.text = element_text(face = 4, hjust = 0),
        panel.grid.major.x = element_blank(),
        panel.grid.minor.x = element_line(colour = "grey65", linetype
= 1),
        panel.grid.minor.y = element_blank(),
        legend.position = "bottom",
        legend.title = element_text(face = 2),
        legend.text = element_text(lineheight = 1),
        legend.background = element_blank(),
        axis.title.y = element_text(angle = 0, vjust = 1, face = 2),
        axis.title.x = element_text(hjust = 0.5, face = 2, margin =
margin(10,0,0,0)),
        plot.title = element_text(face = 4),
        strip.text.y = element_blank())

ggsave(file = "SSF step length interaction males.png", width = 200,
height = 150,
        dpi = 300, units = "mm")

### Calculating tracking consistency and time lag ###

#Load in packages
library(ggplot2)
library(scales)
library(dplyr)
library(move)
library(adehabitatHR)
library(ggspatial)
library(rgeos)
library(maptools)
library(circular)

# read in data file
animal.data <- read.csv(file = "Movement_Data_Corridor_3.csv")
# review the dataset
names(animal.data) # view the column names
# overview of dataset
summary(animal.data)

#get time and date in correct format and add to data (datetime)
animal.data$datetime <-
as.POSIXct(as.character(paste(animal.data$date, animal.data$time)),
tz = 'UTC', format="%d/%m/%Y %H:%M:%S")

```

```

# create a new data object, called animal.clean
# only includes useful columns
animal.clean <- animal.data %>%
  dplyr::select(animal,
                x, y,
                datetime)
# check top of new object
head(animal.clean)
# check bottom of object
tail(animal.clean, 10)
# make sure R understands it is working with dates and times
animal.clean$datetime <- as.POSIXct(animal.clean$datetime,
                                     format = "%Y-%m-%d %H:%M:%S",
                                     tz = "Europe/London")

# check that the datetime has changed
summary(animal.clean)

# Create the consistency of tracking graph
ggplot(animal.clean) +
  geom_point(aes(x = datetime, y = animal)) +
  xlab("Month") + ylab("Snake ID") +
  theme_bw()

ggsave(file = "Tracking consistency.png", width = 200, height = 150,
        dpi = 300, units = "mm")

# Create density time lag
animal.clean %>%
  group_by(animal) %>%
  mutate(time.lag = as.numeric(difftime(datetime,
                                       lag(datetime),
                                       units = "hours")))) %>%

  ggplot(aes(x = time.lag, color = animal, fill=animal)) +
  geom_density(alpha=0.15, fill="lightgrey") +
  scale_x_log10() +
  labs(color= "Snake ID") +
  labs ("Snake ID") + xlab("Time lag (hours)") + ylab("Density")+
  theme(legend.position="right")+
  scale_color_manual(values =
c("#D55E00", "#E69F00", "#0072B2", "#009E73", "#F0E442", "#56B4E9", "#CC79A
7"))+
  theme_bw()

ggsave(file = "Time lag.png", width = 200, height = 150,
        dpi = 300, units = "mm")

#Calculates the mean, standard deviation, min and max values for time
lag.
range(data$time.lag, na.rm = TRUE)
lag.mean <- round(mean(data$time.lag, na.rm = T), digits = 2)
lag.stderr <- round(std_err(data$time.lag[!is.na(data$time.lag)]),
digits = 2)
lag.max <- round(max(data$time.lag, na.rm = T), digits = 2)
lag.min <- round(min(data$time.lag, na.rm = T), digits = 2)

```