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A reliance on human habitats is key to the success of an introduced predatory reptile

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25 Abstract

26 Understanding the success of animals in novel environments is increasingly important as human-mediated introductions continue to move species far beyond their natural ranges. Alongside these introductions, 27 inhabited and agricultural areas are spreading, and correspondingly most animal introductions occur in 28 populated areas. Commensal species which can live alongside humans by making use of specific 29 30 conditions, structures, or prey, have a significant advantage. Introduced mammal species often use anthropogenic features in their environment and demonstrate a higher tolerance of human disturbance, but 31 32 their importance remains understudied in ectotherms. The Aesculapian snake (Zamenis longissimus) is an ectotherm which has been introduced beyond the northern extremities of its natural range. To understand 33 their persistence, we radio-tracked snakes daily over two active seasons, including high-frequency 34 35 tracking of a subset of males. We investigated snake home range size using Autocorrelated Kernel Density 36 Estimators (AKDE). Using AKDE-weighted Habitat Selection Functions we identified preferences for 37 habitat features in a mosaic of habitats, and we used Integrated Step Selection Functions to further explore how these features influence movement. We revealed a particular preference for buildings in male snakes, 38 while females preferred woodland. We demonstrate that the success of this ectothermic predator is likely 39 40 tied to a willingness to use human features of the landscape.

41 Introduction

Through time, the areas inhabited by species are pushed and pulled in many directions by climate, habitat 42 changes, interactions with other species, and human transport. The latter has become a particularly 43 44 powerful force, introducing species to distant, novel habitats where they are exposed to a range of entirely 45 different physical and climatic processes as well as different biotic interactions to those in their native ranges. Not all species are equally successful when faced with such pressures. Identifying the key 46 47 characteristics underpinning the success or failure of species in novel environments can help predict 48 winners and losers in a future where all animals face increased challenges (Moyle & Marchetti, 2006). 49 Through the tracking of animal movements, we can understand traits which are key to success in 50 unfamiliar locations, such as colonisation and dispersal abilities, and habitat requirements (Bubb, Lucas & 51 Thom, 2002; Bartoszek et al., 2021; Kays et al., 2022). Using these insights, we can begin to explore how 52 introduced species adapt to and impact their new habitats.

Many introduced species demonstrate a willingness to utilise human features, including fragmented landscapes and anthropogenic structures, to travel and hunt (Andersen et al., 2017), and have generally demonstrated greater tolerance of human disturbance than their native counterparts (Bielen et al., 2016). Using anthropogenic features is advantageous because non-native species are most likely to be introduced

in or near human-impacted habitats, and it is frequently generalist species that capitalise on these disturbed habitats and make good invaders (Marvier, Kareiva & Neubert, 2004). While much of the available literature focuses on terrestrial endotherms and their adaptability in the face of human dominated landscapes, comparatively little focuses on ectotherms – particularly snakes (Liu et al., 2020). This is despite several prominent examples of introduced snakes (albeit in more natural landscapes) having considerable impacts on the native fauna (Rodda & Savidge, 2007; Dorcas et al., 2012).

63 Snake introductions are not limited to warm climates. Aesculapian snakes (Zamenis longissimus (Laurenti, 1768)) are a constricting species in the family Colubridae. Native to mainland Europe, they range from 64 France in the West to Iran in the East (Musilová, Zavadil & Kotlík, 2007). The species previously 65 66 occupied a larger part of Northern Europe, only recently going extinct in Denmark during the early 1900s (Allentoft, Rasmussen & Kristensen, 2018), with remaining relict populations in Germany, Switzerland, 67 68 the Czech Republic, and Poland. Aesculapian snakes have been introduced twice to the UK in modern 69 times (Allentoft, Rasmussen & Kristensen, 2018). Snakes were introduced to Colwyn Bay, North Wales 70 following an escape from the Welsh Mountain Zoo in the 1970s. This population represents the 71 northernmost modern population of Aesculapian snakes, and its persistence here raises the question of 72 how a species can expand northward, despite the constraints of ectothermy.

73 Over several decades, and especially since the advent of surgically implanted transmitters (Reinert & 74 Cundall, 1982), radiotelemetry has become the backbone of snake spatial ecology. However, despite 75 technological and methodological advancements, few studies have capitalised on recent advances in 76 techniques and analyses to explore the full potential of telemetry data to illuminate the spatial ecology of 77 reptiles. Much of the literature still uses outdated techniques and analyses to calculate habitat selection 78 and home range size (Silva et al., 2020). Home range estimation measures such as minimum convex 79 polygons and kernel density estimators have been continued to be used in determining the home range of 80 animals (Silva et al., 2020). These methods assume independent and identically distributed data, and do 81 not account for autocorrelation, where data points close in time are also close in space (de Solla, 82 Bonduriansky & Brooks, 1999). This was generally acceptable for studies of animals which exhibit 83 frequent movement, especially because of the large time lag between points that result from manually 84 relocating the animal using VHF telemetry. However, for studies of animals which spend long periods 85 inactive, such as snakes, autocorrelation presents a major concern and renders traditional home range 86 estimators unreliable (Silva et al., 2020). Therefore we incorporated the novel approach of Autocorrelated 87 Kernel Density Estimation (AKDE), which overcomes the limitations of traditional estimation techniques 88 in that it accounts for autocorrelation, and these models present the additional benefit of providing 89 confidence intervals for the estimates of home range size provided (Silva et al., 2022). Another continued 90 limitation in most telemetry studies of reptiles involves short tracking durations and infrequent tracking

91 schedules, often ranging from once-daily to weekly tracking. Here, we included a two-hour daily tracking 92 schedule in order to not only distinguish home range sizes more accurately but also to discern dispersal 93 habitat selection. Using an advanced analysis called Integrated Step Selection Functions (ISSF) enabled 94 the modelling of movement and habitat choice simultaneously.

95 The overall aim of this study was to investigate the spatial ecology of an introduced predator, adapted to a 96 warmer climate but existing in cool North Wales. We used radiotelemetry to determine how these animals 97 use their new range, and we set out to discover the home range and space use requirements of both male 98 and female Aesculapian snakes. Our second goal was to discover the habitat preferences of this species, 99 which is crucial to understanding its survival. As we had experienced snakes entering buildings and 100 vegetation piles, we hypothesised that snakes may be reliant on human features of the landscape. Finally, 101 we were keen to know the dispersal capabilities of this species. We wanted to learn which habitats represent pathways to mobile snakes, allowing us to infer their likely routes should this population spread 102 103 into the surrounding area. We hypothesised that hedgerows, as linear features in the habitat, would 104 represent pathways for snakes travelling longer distances.

105

106 Methods

107 Study Area and animals

108 The study site (approximately 1.72 km², see electronic supplementary material) is located between the 109 town of Colwyn Bay and the village of Mochdre, North Wales, UK (53.28–53.29°N, -3.74–3.76°W). The 110 area consists of a mosaic of habitats, including housing, with meadows and pastures separated by 111 hedgerows. Most pastures are grazed periodically by sheep and cattle. The site also includes the Welsh Mountain Zoo covering an area of 0.15 km^2 . The Zoo grounds are highly disturbed because of the constant 112 113 maintenance involving the removal of trees or vegetation, landscaping or building of structures. There is 114 also a patch of woodland in the north corner. Most of the animal faecal matter and vegetation waste is 115 transported to a large dung heap in the southeastern corner of the zoo. Patches of deciduous forest and 116 small patches of gorse scrub are scattered over the entire study site, and a small patch of woodland to the 117 east of the Zoo was in the process of being removed for a new development in 2022. Roads are found throughout, with busy roads surrounding the zoo and the connecting meadows and pastures, with a dual 118 119 carriageway (A55) at the site's northernmost extremity.

We implanted 21 adult Aesculapian snakes with radio transmitters during June – October 2021 and May –
 September 2022 (see supplementary material for tracking and capture summary). Our sample consisted of

13 males and eight females. Snakes were caught by hand, either during dedicated surveys, 122 opportunistically, during radio-tracking activities, or following notification by members of the public. 123 Two tracked individuals were caught by keepers at the Welsh Mountain Zoo during their daily activities. 124 125 Because of the difficulty of finding Aesculapian snakes, which in this population takes approximately 126 eight hours of searching per adult snake found, we radio-tracked any available adult snakes with sufficient 127 body diameter to carry a transmitter. Snakes were transported to Bangor University for transmitter 128 application, and we collected morphometric data including snout-vent length (SVL), tail length (TL) and 129 mass (see supplementary material). We attempted to minimise the time snakes were kept in captivity for implantation procedures (n = 21 implantations, mean = 7.34 ± 6.7 days held, range = 1 - 23 days). Snakes 130 were held in 70L plastic boxes (710 x 545 x 190 mm) in a temperature-controlled room at 21°C with 131 132 suitable refuge and water provided ad libitum.

Depending on their size, snakes were implanted with 1.2, 1.4 or 1.6 g Holohil BD-2T radio transmitters 133 134 (Holohil Inc, Canada) following Reinert & Cundall (1982), using isoflurane anaesthetic and butorphanol 135 analgesia, with an internal securing stitch (Alworth, Hernandez & Divers, 2011). Post-implantation, 136 snakes were kept overnight at a constant 21°C and released the following day. One snake (F159) was held 137 for an additional day post-surgery to ensure wound closure. Snakes were released at their exact point of capture in dry conditions warmer than 14°C. The only exception was M180 who was caught basking on 138 top of a hedge in a residential garden. The homeowner requested we release the snake a short distance 139 140 from their garden, and we released him approximately 30 m away in a hedgerow. As snakes appeared to 141 be behaving normally immediately after release, we began tracking the following day and did not discard 142 any data.

143 **Radiotelemetry**

We employed two different tracking regimes. In order to assess longer distance movements and home range sizes, snakes were located twice daily as part of two daily tracking rounds, the first beginning at 10:00 and a second at 14:00. As we were a small team tracking many snakes, the timings of the tracks were not precise, but animals were usually tracked once in the morning and once in the afternoon, and almost always twice daily. See supplementary material for tracking periods and time lags.

In 2022 a subset of seven male snakes were located five times daily in order to determine what type of habitat the snakes use when they are moving, with the greater tracking frequency allowing us to capture more points in the movement pathway. These snakes were tracked in sessions beginning at 0900, 1100, 1300, 1500 and 1700. One female (F203) was tracked five times daily between 14/05/2022 and 14/06/2022, before switching to twice daily. After 20/08/2022, we began tracking the four male snakes with remaining transmitter battery twice daily (see electronic supplementary material). When we located a

155 snake, we recorded the temperature, humidity, and location, and noted any behaviour. We used a Garmin 156 GPSMAP 64S to collect GPS locations. To avoid disturbing the snake and thus influencing their 157 behaviour, we attempted to keep 10 metres between observers and tracked snakes, but within the confines 158 of narrow gardens this was not always possible.

159 **Snake home range estimation**

160 To implement Autocorrelated Kernel Density Estimations (AKDE), we used the *ctmm* package 161 (Calabrese, Fleming & Gurarie, 2016) and R v4.2.1 (R Core Team, 2022, p. 4) to fit continuous time stochastic process movement models to our snake movement data. We first checked individuals for range 162 163 residency to ensure their range is no longer expanding by calculating the semi-variance function and 164 visualising it using variogram analysis (Fleming & Calabrese, 2021). We removed individuals that did not demonstrate range-residency from the home range analysis. We fitted multiple movement models and 165 166 used AICc to identify the model best fitting the autocorrelation structure for each snake. These were either 167 the Ornstein-Uhlenbeck (OU) model where the animal exhibits Brownian motion restricted to a finite 168 home range, or the OUF model with continuous-velocity motion restricted to a finite home range, or 169 Independent Identically Distributed (IID). These prototype models are either isotropic, where there is 170 equal diffusion in every direction, or anisotropic, where diffusion varies depending on direction (Calabrese, Fleming & Gurarie, 2016). For optimal performance we estimated autocorrelation and 171 covariance bias using pertubative hybrid residual maximum likelihood (pHREML), accounting for both 172 small absolute sample size and small effective sample size (Fleming et al., 2019). Absolute sample size 173 174 refers to the total number of times the animal was located during the tracking period, while effective sample size is the entire tracking duration divided by how long it takes, on average, for the animal to cross 175 176 its linear home range. We then fit AKDEs using the guidance provided by Silva et al., (2022). We used weighted AKDEc and pHREML to estimate home range size, which reduces oversmoothing of range 177 178 limits, particularly in cases with small effective sample sizes (Silva et al., 2022). It also helps to address 179 irregular sampling. Silva et al. (2022) recommend pHREML and AKDEc for effective sample sizes (range 180 crossings) below 20, which applied to most individuals. Parametric bootstrapping can also be used to 181 reduce estimation error, and we used ctmm.boot in the *ctmm* package to apply parametric bootstrapping to 182 individuals with low effective sample sizes (Silva et al., 2018; Thompson et al., 2021).

183 Space use

184 In recent years there has been a rise in the use of dynamic Brownian Bridge Movement Models 185 (dBBMMs) to estimate the home ranges of animals, but these estimators are not suitable for this purpose 186 (Alston et al., 2022b). As these models are occurrence distribution estimators and not range distribution estimators, these models use animal locations over time to interpolate where animals might have been during a tracking period, rather than extrapolating to their entire range (Alston et al., 2022b). However, dBBMMs have utility in estimating space use during the study period, and allow for comparison with other studies, giving a valuable impression of snake spatial ecology during the study period. As many snakes were unlikely to have sufficient tracking durations to facilitate home range estimation, we use estimates of space use derived from dBBMMs.

We estimated snake space use using the R package *move* v4.1.10 (Kranstaber, Smolla & Scharf, 2022). As snakes were generally active for a few days before spending between a few days and a week inactive, we specified a moving window of 11. With our twice daily tracking regime, this allowed us to detect variations in the behavioural state of snakes over a six day period (D'souza et al., 2021). We chose a margin size of three to allow detection of active vs inactive states (D'souza et al., 2021), and used the mean GPS error of our snake locations as the telemetry error. We used two daily tracks to model space use across all individuals.

200 Habitat selection

All analyses were conducted using R v4.2.1 (R Core Team, 2022). For all habitat use analyses, we used custom shape files of habitat types created in QGIS Using modified code from Smith et al (Smith et al., 2021) and Hodges et al (Hodges et al., 2022), we converted our raster layers into layers with continuous gradients denoting the Euclidean distance to habitat features. These layers were then inverted to avoid zero-inflation and to ensure that the resulting outputs were easy to interpret, as positive values indicate selection.

207 Integrated Resource (Habitat) Selection Functions

208 Traditional resource selection function analyses, now termed habitat selection functions (Fieberg et al., 209 2021), do not allow for autocorrelated data and assume independence between each point at which an 210 animal is located. However, for high-resolution GPS location frequencies, or for animals which move 211 infrequently, points are not independent from each other. To avoid the need to thin data to ensure 212 independence of points, we utilised habitat selection functions informed by our AKDEs, which down-213 weight autocorrelated points rather than discarding them (Alston et al., 2022a). We used rsf.fit within the 214 *ctmm* package (Fleming & Calabrese, 2021) to fit integrated resource selection functions to our snake 215 tracking data, with simultaneously estimated spatial constraints. We used the Monte Carlo numerical 216 integrator for likelihood evaluation, with a numerical error threshold of 0.05 for the parameter estimates 217 and log-likelihood.

Integrated Step Selection Functions

219 We used Integrated Step Selection Functions (ISSF) to analyse how habitat types influenced the 220 movements of Aesculapian snakes at the population scale. This allowed us to incorporate the movements 221 of all tracked individuals, even those with short tracking durations that did not demonstrate range-222 residency. We split the data into male and female snakes and adapted code from Smith et al (2021) and 223 Muff et al. (2019) to run mixed conditional Poisson regression models essentially operating as 224 "population-level ISSFs" on our twice-daily tracking data. The first and third daily tracks of snakes which 225 had been tracked five times daily were used to ensure comparability with our twice daily data. Using the INLA package v22.05.07 (Rue, Martino & Chopin, 2009) we ran a population-level ISSF to ascertain 226 227 either association or avoidance of our eight habitat classifications. We removed zero distance steps (non-228 moves) from this analysis. We generated 200 random points per move, for step length we used a Gamma 229 distribution and for turn angle Von Mises (Smith et al., 2021; Hodges et al., 2022), to facilitate 230 comparison between locations the snakes selected and locations they did not. We created eight singlefactor models, one for each habitat type, and all models included the interaction of turn angle and step 231 232 length. As per Muff et al. (2019) the stratum-specific random effect of step was set to 0.0001. In keeping 233 with Smith et al. (2021), we utilised a Penalised Complexity prior, PC (1, 0.05) for the random slope, 234 which was individual, and uninformative normal priors were used for the fixed effects. Using the INLA package v22.05.07 (Rue, Martino & Chopin, 2009), we used nested Laplace approximations in fitting 235 236 these models.

237 For the male snakes tracked five times daily, we ran both individual ISSFs as well as the "population-level ISSFs" described above to investigate whether Aesculapian snakes demonstrated attraction to or 238 239 avoidance of habitat types at the scale of the whole population. For individual selection, we created ISSFs 240 using INLA package v22.05.07 (Rue, Martino & Chopin, 2009), filtering steps using a resample rate of 241 two hours with a tolerance of four hours to avoid bias from unexpected overnight movements. We created 242 nine single-factor models, one for each habitat type, and one representing the null model. The individual 243 habitat models also included the interaction of turn angle and step length, while the null model only 244 included the interaction of step length and turn angle. Otherwise, we used the same settings as described 245 above. We used AIC scores to determine which features most strongly influenced the habitat selection of 246 Aesculapian snake individual movements from our ISSF. Models with the lowest AIC score or scores < 2247 greater than the lowest were considered to have the largest influence.

248 Seasonality and shelter locations

We used two measures to determine seasonal behaviour changes in Aesculapian snakes, mean daily displacement and dBBMM-derived motion variance (Hodges et al., 2022). We use dBBMMs to visualise the space use of tracked snakes over the tracking period and ascertain areas of high use and re-use that are of particular significance to Aesculapian snakes. We also use the estimates of motion variance they provide to determine periods of heightened activity during the tracking period (Hodges et al., 2022).

254 Although mean daily displacement (MDD) has limitations, we were unable to estimate speed or distance 255 travelled using continuous-time movement models [10], likely due to the relative infrequency of our data 256 points compared to high-resolution GPS data. Despite the shortcomings of MDD (Rowcliffe et al., 2012), 257 we kept to a strict tracking schedule of at least two tracks per day for all individuals, allowing increased confidence in the MDD estimates (see electronic supplementary material). To investigate seasonality, we 258 259 filtered the first and third daily tracks of snakes which received five tracks per day to allow comparison between all individuals. We summed the movement distance across these two daily tracks to create our 260 values for daily displacement. We opportunistically collected observational data on the breeding 261 262 behaviour of this population during tracking activities, which allowed us to better inform the dates of the mating and egg-laying seasons. 263

To understand areas snakes used for long periods, we first created move objects in R using twice daily tracking data for all 21 individuals with the package *move* v4.1.10 (Kranstaber, Smolla & Scharf, 2022). Using the *recurse* package v1.1.2 (Bracis, Bildstein & Mueller, 2018), we set a radius of five meters around each location a snake visited. We recorded the amount of time each snake spent in the same location for multiple fixes as time spent stationary. Finally, we used the recurse package to visualise places the snakes had spent long periods, and recorded what these locations were by overlaying the GPS locations on a map. We verified the locations using our behavioural notes.

271 Limitations and data statement

In line with the STRANGE framework (Webster & Rutz, 2020), we recognise that there may be bias in the trappability and self-selection of our sample of snakes. Snakes were frequently near people or their dwellings when captured. Seven of the 13 male snakes were captured at different times under one tarpaulin covering a wood pile in the garden of a residential home, while three of eight females came from one garden containing multiple mature compost heaps. As many snakes were found near each other, there is also a higher likelihood they are related.

All Figs were created using R v4.2.1 (<u>https://r-project.org/</u>). For data manipulation we used the *amt*package v0.1.7 (Signer, Fieberg & Avgar, 2019) and the *dplyr* package v1.0.10 (Wickham et al., 2022).
For data visualisation we used *ggplot2* v3.3.6 (Wickham, 2016). For visualising movement data and

- creating tracks we used move v4.1.10 (Kranstaber, Smolla & Scharf, 2022). All data and code used in this
- study are available from the online repository figshare (link to be added).

283 **Results**

284 Movements

We tracked 13 adult male and eight adult female Aesculapian snakes between June and October 2021 and May and September 2022. The average tracking duration was $56.67 \pm SE 7.85$ days (range 4 – 126 days). We collected a total of 3232 snake locations, which included 947 relocations (a move from the previous location). The mean daily displacement (MDD) for six male snakes on the twice daily tracking regime was 38.45 ± 21.33 m, and for the seven males on the five times daily regime it was 52.34 ± 26.43 m. The MDD of eight females tracked twice daily was 26.14 ± 18.55 m.

291 Snake home ranges

292 Eight males and three females were found to have stable home ranges using variogram analysis (see 293 electronic supplementary material). The remaining ten individuals did not reach an aysmptote (Fleming et 294 al., 2014). For these individuals, the short tracking durations meant that there was insufficient information 295 to inform our home range estimation model, and they were excluded from Autocorrelated Kernel Density 296 Estimation (AKDE). Full model results for all individuals can be found in Table 1. The mean effective 297 sample size for snakes included in the AKDE analysis was 12.92 ± 8.57 (range 4.29 - 35.57). These Figs 298 are relatively low and demonstrate that using the pHREML method and weighting the AKDEs was 299 justified (Silva et al., 2022). The mean 95% AKDE estimate for home range size for the three range resident females was 23.32 ± 29.74 ha (range 0.28 - 65.31 ha). For eight range resident males it was 28.86 300 301 \pm 28.42 ha (range 2.05 – 92.16 ha). For range resident snakes (Fig 1), the top models were Ornstein-302 Uhlenbeck (OU) or Ornstein-Uhlenbeck foraging (OUF). Two individuals, F159 and M218, had low effective sample sizes of six and 4.3 respectively, with pHREML bias in the order of 3% or higher (Table 303 1), and we applied parametric bootstrapping to these individuals. All models reflected elliptical home 304 305 ranges (anisotropic) except for F158 which was more circular (isotropic). The traditional KDE approach 306 of using Independent Identically Distributed (IID) points proved ineffective and the IID models had high 307 dAICc values (see electronic supplementary material).

Table 1: Results of the snake AKDE home range analysis. Effective sample size refers to the number of times the animal crossed its home range during the tracking period, while absolute sample size is the total number of observations (fixes). Contour area estimates of home range for individuals presented in

- 311 hectares. F159 and M218 had parametric bootstrapping applied to reduce error on their home-range
- 312 estimates and the estimates displayed are post-bootstrapping.

ID	AICc top model	Effective	Absolute	95%	95%	95%	pHREML	Parametric
		sample	sample	AKDE	AKDE	AKDE	bias	bootstrap
		size	size	lower CI	estimate	upper		bias
				(ha)	(ha)	CI (ha)		
F158	OU	8.72	102	1.97	4.37	7.72	0.013	-
F159	OUF anisotropic	4.71	102	20.10	64.75	135.03	0.028	0.0096
F177	OU anisotropic	35.57	126	0.19	0.28	0.38	0.001	-
M031	OU anisotropic	19.44	165	1.24	2.05	3.05	0.003	-
M137	OU anisotropic	9.36	209	9.98	21.44	37.20	0.011	-
M139	OU anisotropic	8.69	167	7.83	17.41	30.75	0.013	-
M154	OU anisotropic	7.66	302	4.54	10.75	19.59	0.017	-
M180	OU anisotropic	14.89	96	1.46	2.61	4.10	0.005	-
M202	OU anisotropic	8.83	457	23.37	51.57	90.74	0.013	-
M209	OU anisotropic	18.74	423	19.72	32.89	49.37	0.003	-
M218	OU anisotropic	4.08	192	100	120.04	261.50	0.054	0.0147

313

314

Fig 1. AKDE home ranges for tracked snakes that demonstrated range-residency. A-D) Male snakes.
E, F) Female snakes. Darkest shading in the centre represents the lower confidence interval for the 95% home range contour, medium shading is the 95% contour, and the lightest shading is the upper confidence interval. Points represent location data of each animal. While F203 did not demonstrate range residency, we plot the data here for illustration purposes as she was tracked for a relatively long period of 65 days.

320

321 Snake space use

We estimated space use using dBBMMs (Table 2). We excluded three snakes with tracking durations less than 14 days (F212, F219, and M073) from the following means as their space use estimates would likely skew the results. For females, the mean area of the 95% confidence occurrence distributions was $2.09 \pm$ 3.79 ha (range = 0.02 - 10.51 ha). The mean area of the 95% confidence occurrence distributions for males was 6.34 ± 7.10 ha (range 0.46 - 20.72 ha).

327

328 Table 2. dBBMM occurrence distributions and mean daily displacement (MDD) for the Aesculapian

329 snakes tracked in this study.

	90% (ha)	95% (ha)	99% (ha)	Transfilme		MDD (m)	Maximum
ID				duration	Total distance		daily
ID					moved (m)		distance
				(days)			(m)
F050	0.02	0.05	0.16	28	216.20	7.74	56.78
F142	0.02	0.02	0.04	33	264.26	8.05	58.09
F158	0.55	1.30	3.23	50	1028.29	20.57	92.10
F159	5.91	10.51	18.42	61	3673.04	60.38	364.43
F177	0.21	0.32	0.59	90	782.51	8.68	44.67
F203	0.19	0.32	0.92	65	1282.96	19.70	72.06
F212	0.07	0.09	0.13	4	157.93	38.04	64.73
F219	0.01	0.01	0.02	12	555.29	46.00	244.47
M031	0.63	1.03	1.97	33	1135.56	34.20	129.11
M073	9.03	12.48	20.82	9	698.28	78.71	206.39
M074	0.01	0.01	0.02	30	179.99	5.97	64.96
M137	1.82	4.51	14.49	126	3894.85	30.95	382.88
M139	2.27	7.21	22.72	95	3903.90	41.10	559.30
M149	1.56	2.76	6.41	37	1706.27	46.37	336.90
M154	1.79	3.67	7.57	74	2427.55	32.70	107.16
M178	0.29	0.46	0.87	83	999.82	12.04	255.31
M180	1.31	2.13	4.48	57	1225.27	21.54	125.12
M202	5.55	10.75	25.43	112	7935.06	70.85	566.25
M209	14.10	21.00	35.59	107	7387.04	69.03	365.16
M217	0.35	1.85	5.27	17	1477.92	86.94	383.95
M218	11.94	20.72	43.71	67	4469.91	66.73	586.54

330

331 Individual habitat selection via AKDE-weighted RSF

We had sufficient data to inform range-residency and perform the habitat selection analysis on three female and eight male Aesculapian snakes. These parameter estimates for resource selection are visualised in Fig 2. The results for the remaining snakes can be found in the supplementary material. In male snakes, buildings were the most commonly selected-for habitat type with five of eight individuals demonstrating positive selection for buildings and two more strongly suggesting it without definitive evidence (Fig 2). M137 and M139 showed a preference for woodland, while M202 and M209 were associated with pasture.

One chose gardens (M180), one selected meadows (M202), and similarly only (M154) showed a preference for hedgerows. For females, F159 showed avoidance of pasture. We were unable to determine individual preference or for any habitat type for females in this analysis. With regards to males avoiding habitat types, three individuals (M031, M180 and M202) avoided roads, while M202 avoided woodland.

342

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Fig 2. Coefficients from the weighted AKDE habitat selection functions for range resident snakes.
Each plot displays the habitat selection of one individual snake. Positive values indicate selection for a
habitat type, while negative values indicate avoidance. Error bars represent 95% confidence intervals.

347 **ISSF at the population scale**

The ISSF analysis suggests woodland is of importance for females at the population-level (Fig 3). Males demonstrated habitat generalism, showing selection for meadows, scrub, road surfaces, and possibly hedgerows, but appearing to select areas nearer to buildings and gardens most strongly (Fig 3). We were unable to detect differences in step length associated with different habitat types for either females or males at the population scale (see electronic supplementary material).

353

Fig 3. Results of the ISSF analysis at the population-level for female snakes (n = 8) and male snakes
 (n = 13). Bars represent 95% confidence intervals. Positive values indicate selection toward a particular
 habitat type, while negative values indicate avoidance.

357 Step length from five times daily tracking

We included the data from six of the seven males that were tracked five times daily, excluding M074 who spent 29 of 30 tracking days stationary. We investigated the influence of habitat type on the step lengths of individual snakes (Fig 4). For M202, shorter steps were associated with buildings and roads. For M218, both proximity to pasture and hedgerows were associated with shorter steps.

We also determined which features influenced the habitat selection of snakes. The top model was pasture for M218. Gardens were top or second for M154 and M217. Hedgerows were top or second for M154 and M209, while M207. M031, M154, and M202 were influenced by buildings (see electronic supplementary material). Model selection results do not necessarily equate to definite selection or avoidance, however. At the individual level, two snakes, M154 and M202, preferred to be closer to meadows and pasture. M218 showed a positive association with hedgerows and scrub. None of the remaining males tracked five times

368 daily showed definitive habitat association in this analysis. We also ran the population-level analysis for 369 this group, who demonstrated a preference for hedgerows, buildings and scrub, but we found no 370 significant influence of habitat type on step length using the population-level analysis with this group (see 371 electronic supplementary material).

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- 373

Fig 4. Individual integrated step selection functions demonstrating the interaction between step length and habitat types for Aesculapian snakes under the five times daily tracking regime. Positive values indicate longer steps associated with a habitat feature, and negative values indicate shorter steps. Error bars indicate 95% confidence intervals. Circles indicate the features which were included in models with the lowest AIC score or scores less than two higher.

379 Seasonality

- 380 Female movement showed a visible peak in motion variance during the egg-laving season from July to 381 mid August (Fig 5). The mean daily displacement (MDD) of females during the egg-laying season was 34.05 ± 75.45 m/day compared to 12.52 ± 32.33 m/day during the rest of the year (Fig 6). Across all 382 females there was only one day where an individual moved > 100 m outside of the egg-laying season, and 383 384 females were sedentary outside of this period. We discovered eggs inside the compost heap of a residential 385 property immediately after F177 left it on 10/08/2021. F159 made an uncharacteristically long 364m move 386 in mid-July that we interpret as nest searching, before spending three days (13/07/2021 - 16/07/2021)387 inside the dung pile within the Welsh Mountain Zoo. While we could not locate her eggs despite extensive 388 search, this may be due to the size of the pile, which is approximately 10 m across. We found a separate clutch of eggs inside this pile in 2019, confirming that it is an egg-laying site for the species. One further 389 390 Aesculapian snake egg was found by Zoo staff in a pile of wood chippings 20 m from the dung heap on 391 the Zoo site in 2021.
- 392
- Fig 5. Motion variance plot for females and males through the study periods in 2021 and 2022. Peaks
 represent increased movement distances.
- 395

Fig 6. Raincloud plot visualising the mean daily displacement of eight tracked female Aesculapian snakes and 13 tracked male Aesculapian snakes through 2021-2022. Each point represents the distance moved by a snake on an individual day. Non-moves are excluded from the box and density plots, with numbers inside the box showing the number of moving days in each season. Days without movement are plotted to the far left along with a count. Mean daily displacement for each season, with non-moves included, are printed along with a small black arrow. The egg-laying season (July 1^{st} – August 16^{th}) and the mating season (15^{th} May – 30^{th} June) are compared with the rest of the active season for females and males respectively. Fig created using code adapted from (Hodges et al., 2022).

The males showed a visible peak in motion variance the mating season between mid May and the end of June (Fig 5). The MDD of males during the mating season was 68.7 ± 112.22 m/day compared to $26.3 \pm$ 58.39 m/day during the rest of the year (Fig 6). Males only moved distances > 500 m per day during the mating season, despite occasional periods of high activity in mid-summer. We observed one tracked male mating on 13/06/2021 and another on 24/05/2022. We witnessed one of our tracked males in combat with an unknown male on 15/06/2022. These observations reinforce our understanding of the timings of the mating season of this species in Wales.

411 **Snake mortality**

Of our sample of 21 tracked snakes, five died during their tracking periods, and one died after tracking was completed. In total, three females died. F177 was tracked during 2021 until the transmitter ran out of battery, and was then found dead the following year on 15/08/2022 after a car strike (see supplementary material). F142 was also killed by a car strike on 07/07/2021 after being tracked for 33 days, on the same two-laned stretch of road as F177. Both snakes were gravid at the time of death, containing four and seven well-developed eggs respectively. Lastly, F159 was cannibalised by a tracked male (M137) in August 2021 (Major et al., 2023).

Three of 13 male snakes died during the study. In 2021, M073 was predated by buzzards, with his transmitter signal discovered in a pine tree containing a buzzard nest, approximately 30 m high up. M149 died from mammal predation. The snake was found at the edge of a meadow with approximately one metre of trampled grass in all directions with a broken neck. Small sections of the snake had been consumed. We suspect either a stoat, badger, or domestic cat was responsible. Finally, in the 2022 season, M031 was killed by a car strike on the entrance road within the Welsh Mountain Zoo grounds.

425 **Time spent sheltering**

426 All snakes spent time stationary, being located at the same location for at least two tracks in succession.

427 The mean time spent stationary of all females was 4.91 ± 4.04 days (0.5 - 14.27 days). For all males, the 428 mean time spent stationary was 5.14 ± 6.67 days (range 0.82 - 27.61 days). Generally, when snakes were

429 in the same location for multiple successive fixes, they were inside shelter. The exception were two snakes

who were repeatedly found in basking sites in vegetation at the edges of roads (M137 and M218). Females selected a road verge (n = 1), compost or vegetation piles (n = 4), and buildings (n = 3) as repeated or long-term shelter. Males chose a road verge (n = 1), compost or vegetation pile (n = 1), or buildings (n = 10). Five males used two different buildings for shelter, while three males used three different buildings. These shelter sites were often used for long periods, and seven males and seven females spent \geq 10 days in an individual shelter (see supplementary material).

436

437 **Discussion**

438 Our suite of habitat and step selection analyses reveal that male Aesculapian snakes show a distinct preference for buildings in their introduced range in North Wales, with seven of eight individuals in our 439 440 AKDE-weighted habitat selection function selecting buildings as habitat, and our population SSF model highlighted their importance to male snakes. Like many introduced species, Aesculapian snakes were 441 442 introduced close to an urban area following escape from captivity. Urban areas often contain under-443 utilised resources, and introduced species which can capitalise on them have a significant advantage 444 (Mitchell, Folt & Hall, 2021). For snakes, anthropogenic structures such as buildings and culverts provide 445 shelter, thermoregulatory opportunities and egg-laving sites (Keller & Heske, 2000; Lelièvre et al., 2010; 446 Hanslowe et al., 2016; Hodges et al., 2022; Yu et al., 2022). Snakes frequently took shelter in human 447 features of the habitat, and compost heaps, vegetation piles, and buildings represented long-term shelter for female snakes. Females spent long periods inactive during the Spring and early summer, remaining in 448 449 shelter - particularly compost heaps. Males frequently used buildings as shelter sites, with one individual 450 using a hole in a road verge and one a vegetation pile as long-term or revisited shelter sites.

451 We observed Aesculapian snakes actively seeking and returning to use inhabited buildings and were 452 observed climbing large structures to access the attics and wall cavities of houses. This attraction towards 453 anthropogenic features is unusual behaviour compared with native snake species in the UK that often 454 avoid built up urban areas. The Adder (Vipera berus) and smooth snake (Coronella austriaca) are rarely 455 found in human-dominated environments. Grass snakes (Natrix sp. including Natrix helvetica) can be 456 found in anthropogenic environments and will use compost heaps, manmade structures, or ponds in 457 gardens, but their use of anthropogenic features is significantly less extensive (Wisler, Hofer & Arlettaz, 2008; Reading and Jofré, 2009; Löwenborg et al., 2010). With urbanisation continuing unabated, the 458 459 ability to survive in human-dominated landscapes is valuable to individual species and vital for maintaining biodiversity (Collins, Magle & Gallo, 2021). Herpetofauna and invertebrates remain 460 understudied in this realm, and our suite of analytical approaches represents an unusually detailed 461 investigation into the lives of a cryptic reptile species. 462

463 Our evidence here suggests that, like other snakes, Aesculapian snakes have peaks in activity due to their 464 reproductive cycles (Row, Blouin-Demers & Lougheed, 2012; Marshall et al., 2020). The activity of male 465 snakes peaked in the mating season in May and June, coinciding with observations of male-male combat 466 and mating, while females exhibited a definite peak during summer when they travel to lay their eggs. We 467 discovered eggs in rotting vegetation built up by humans - a compost heap, a pile of wood chippings, and 468 a dung heap at the Welsh Mountain Zoo, further demonstrating the importance of human elements of the 469 habitat to this introduced species.

470 Despite their ability to benefit from human features of the landscape, the semi-rural range of this 471 introduced predator also contains dangers. Three of 21 tracked snakes died to road mortality. Road mortalities can be high for juvenile Aesculapian snakes (Kovar et al., 2014), and our study site lacks any 472 473 culverts beneath the roads, which are known to be utilised by snakes for road crossing (Jones et al., 2022). 474 Indeed, road mortality was found to be low for adult Aesculapian snakes in a population where culverts 475 allowed safe passage under roads (Kovar et al., 2014). Two females died on roads while heavily gravid, 476 potentially suggesting an increased risk of road mortality when travelling to lay eggs. Reptiles are known to increase their movement distances in highly disturbed areas, despite keeping smaller home ranges 477 478 (Doherty, Hays & Driscoll, 2021), further exacerbating the risk of road mortality. Three snakes 479 demonstrated avoidance of roads in this study, suggesting they may be responsible for limiting the 480 expansion of this species, although this is more likely the case for wider roads (Roe, Gibson & Kingsbury, 481 2006; Bauder et al., 2021). Two other mortalities in this study were caused by a mammalian predator and 482 a buzzard, and one was cannibalised by an Aesculapian snake (Major et al., 2023).

483 Conclusion

484 In summary, this study demonstrates the importance of human-dominated habitats to an introduced 485 predator. While Aesculapian snakes are present in the fossil record of the UK, they have been absent for 486 likely 300,000 years (Ashton et al., 1994). Worldwide, animal ranges are shifting poleward or to higher 487 elevation as the climate warms dramatically because of human activity (Lenoir & Svenning, 2015). The 488 UK is now home to an increasing number of mobile species which can travel over sea from further South, 489 including numerous moths and butterflies (Sparks et al., 2007), and wetland birds (Hiley et al., 2013). 490 Aesculapian snakes have similarly migrated northward, only via human transport instead of natural means. 491 That said, it seems likely that North Wales represents the northernmost tolerance limit of this species in 492 current climatic conditions. The use of buildings for shelter and vegetation piles for egg laying appear to 493 be important to their success in a temperate climate that is further north than any remaining native 494 populations. However, simply being successful in an area is not evidence to suggest the area contains ideal 495 conditions (Hawley Matlaga et al., 2021), and the broad range of habitats selected by individual snakes in

this study suggest that Aesculapian snakes are adaptable generalists, capable of using mixed habitat andunafraid of using buildings and other features in close proximity to humans.

498

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- 682

683

684







F159

0.05 0.10 -0.05 0.00



M180

10 -6 юн -0.6 -0.3 0.0 0.3

M218









Figure5



Mean Daily Displacement (m)

5