

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

--Manuscript Draft--

Manuscript Number:	PONE-D-24-37502
Article Type:	Research Article
Full Title:	A reliance on human habitats is key to the success of an introduced predatory reptile
Short Title:	Aesculapian snakes use human habitats in their introduced range
Corresponding Author:	Tom Major Bournemouth University Poole, Dorset UNITED KINGDOM OF GREAT BRITAIN AND NORTHERN IRELAND
Keywords:	Aesculapian, snake, Colubridae, spatial ecology
Abstract:	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, inhabited and agricultural areas are spreading, and correspondingly most animal introductions occur in populated areas. Commensal species which can live alongside humans by making use of specific 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 their importance remains understudied in ectotherms. The Aesculapian snake (<i>Zamenis longissimus</i>) is an ectotherm which has been introduced beyond the northern extremities of its natural range. To understand their persistence, we radio-tracked snakes daily over two active seasons, including high-frequency tracking of a subset of males. We investigated snake home range size using Autocorrelated Kernel Density Estimators (AKDE). Using AKDE-weighted Habitat Selection Functions we identified preferences for 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, while females preferred woodland. We demonstrate that the success of this ectothermic predator is likely tied to a willingness to use human features of the landscape.
Order of Authors:	Tom Major Lauren Jeffrey Guillem Limia Russel Rebecca Bracegirdle Antonio Gandini Rhys Morgan Benjamin Michael Marshall John F Mulley Wolfgang Wüster
Additional Information:	
Question	Response
Financial Disclosure	Yes
Enter a financial disclosure statement that describes the sources of funding for the work included in this submission. Review the submission guidelines for detailed requirements. View published research articles from PLOS ONE for specific	

examples.

This statement is required for submission and **will appear in the published article** if the submission is accepted. Please make sure it is accurate.

Funded studies

Enter a statement with the following details:

- Initials of the authors who received each award
- Grant numbers awarded to each author
- The full name of each funder
- URL of each funder website
- Did the sponsors or funders play any role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript?

Did you receive funding for this work?

Please add funding details.
as follow-up to "**Financial Disclosure**

Enter a financial disclosure statement that describes the sources of funding for the work included in this submission. Review the [submission guidelines](#) for detailed requirements. View published research articles from [PLOS ONE](#) for specific examples.

This statement is required for submission and **will appear in the published article** if the submission is accepted. Please make sure it is accurate.

Funded studies

Enter a statement with the following details:

- Initials of the authors who received each award
- Grant numbers awarded to each author
- The full name of each funder
- URL of each funder website
- Did the sponsors or funders play any role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript?

This work was supported by the Knowledge Economy Skills Scholarships (KESS II – case number 80815) and the Welsh Mountain Zoo, awarded to WW and JM for TM's PhD. Additional funding was provided by the Biodiversity and Ecosystem Evidence and Research Needs (BEERN) Programme awarded to TM.

<p>Did you receive funding for this work?"</p>	
<p>Please select the country of your main research funder (please select carefully as in some cases this is used in fee calculation).</p> <p>as follow-up to "Financial Disclosure</p> <p>Enter a financial disclosure statement that describes the sources of funding for the work included in this submission. Review the submission guidelines for detailed requirements. View published research articles from PLOS ONE for specific examples.</p> <p>This statement is required for submission and will appear in the published article if the submission is accepted. Please make sure it is accurate.</p> <p>Funded studies Enter a statement with the following details:</p> <ul style="list-style-type: none"> • Initials of the authors who received each award • Grant numbers awarded to each author • The full name of each funder • URL of each funder website • Did the sponsors or funders play any role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript? 	<p>UNITED KINGDOM - GB</p>
<p>Did you receive funding for this work?"</p> <p>Competing Interests</p> <p>Use the instructions below to enter a competing interest statement for this submission. On behalf of all authors, disclose any competing interests that could be perceived to bias this work—acknowledging all financial support and any other relevant financial or non-financial competing interests.</p>	<p>The authors have declared that no competing interests exist.</p>

This statement is **required** for submission and **will appear in the published article** if the submission is accepted. Please make sure it is accurate and that any funding sources listed in your Funding Information later in the submission form are also declared in your Financial Disclosure statement.

View published research articles from [PLOS ONE](#) for specific examples.

NO authors have competing interests

Enter: *The authors have declared that no competing interests exist.*

Authors with competing interests

Enter competing interest details beginning with this statement:

I have read the journal's policy and the authors of this manuscript have the following competing interests: [insert competing interests here]

* typeset

Ethics Statement

Enter an ethics statement for this submission. This statement is required if the study involved:

- Human participants
- Human specimens or tissue
- Vertebrate animals or cephalopods
- Vertebrate embryos or tissues
- Field research

Write "N/A" if the submission does not require an ethics statement.

General guidance is provided below. Consult the [submission guidelines](#) for detailed instructions. **Make sure that all information entered here is included in the Methods section of the manuscript.**

This work took place with approval from the Bangor University Animal Welfare and Ethics Review Board. Telemetry procedures were conducted under Home Office project licence PC44793B6.

Format for specific study types

Human Subject Research (involving human participants and/or tissue)

- Give the name of the institutional review board or ethics committee that approved the study
- Include the approval number and/or a statement indicating approval of this research
- Indicate the form of consent obtained (written/oral) or the reason that consent was not obtained (e.g. the data were analyzed anonymously)

Animal Research (involving vertebrate animals, embryos or tissues)

- Provide the name of the Institutional Animal Care and Use Committee (IACUC) or other relevant ethics board that reviewed the study protocol, and indicate whether they approved this research or granted a formal waiver of ethical approval
- Include an approval number if one was obtained
- If the study involved *non-human primates*, add *additional details* about animal welfare and steps taken to ameliorate suffering
- If anesthesia, euthanasia, or any kind of animal sacrifice is part of the study, include briefly which substances and/or methods were applied

Field Research

Include the following details if this study involves the collection of plant, animal, or other materials from a natural setting:

- Field permit number
- Name of the institution or relevant body that granted permission

Data Availability

Authors are required to make all data underlying the findings described fully available, without restriction, and from the time of publication. PLOS allows rare exceptions to address legal and ethical concerns. See the [PLOS Data Policy](#) and [FAQ](#) for detailed information.

Yes - all data are fully available without restriction

A Data Availability Statement describing where the data can be found is required at submission. Your answers to this question constitute the Data Availability Statement and **will be published in the article**, if accepted.

Important: Stating 'data available on request from the author' is not sufficient. If your data are only available upon request, select 'No' for the first question and explain your exceptional situation in the text box.

Do the authors confirm that all data underlying the findings described in their manuscript are fully available without restriction?

Describe where the data may be found in full sentences. If you are copying our sample text, replace any instances of XXX with the appropriate details.

- If the data are **held or will be held in a public repository**, include URLs, accession numbers or DOIs. If this information will only be available after acceptance, indicate this by ticking the box below. For example: *All XXX files are available from the XXX database (accession number(s) XXX, XXX).*
- If the data are all contained **within the manuscript and/or Supporting Information files**, enter the following: *All relevant data are within the manuscript and its Supporting Information files.*
- If neither of these applies but you are able to provide **details of access elsewhere**, with or without limitations, please do so. For example:

Data cannot be shared publicly because of [XXX]. Data are available from the XXX Institutional Data Access / Ethics Committee (contact via XXX) for researchers who meet the criteria for access to confidential data.

The data underlying the results presented in the study are available

All data and code are available from <https://figshare.com/s/10b8bafb3ce0069555a1>

<p><i>from (include the name of the third party and contact information or URL).</i></p> <ul style="list-style-type: none">• This text is appropriate if the data are owned by a third party and authors do not have permission to share the data. <p>* typeset</p>	
Additional data availability information:	Tick here if the URLs/accession numbers/DOIs will be available only after acceptance of the manuscript for publication so that we can ensure their inclusion before publication.

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

3

4

5 Tom Major¹, Lauren Jeffrey², Guillem Limia Russel², Rebecca Bracegirdle², Antonio Gandini²,
6 Rhys Morgan², Benjamin Michael Marshall³, John F. Mulley², and Wolfgang Wüster²

7

8 ¹ Department of Life & Environmental Sciences, Bournemouth University, Fern Barrow, Poole,
9 Dorset, BH12 5BB, UK

10 ² School of Environmental and Natural Sciences, Bangor University, Bangor, Gwynedd, LL57
11 2DG, UK

12 ³ Department of Biological and Environmental Sciences, University of Stirling, Stirling, FK9
13 4LA, Scotland, UK

14

15 Corresponding author

16 tmajor@bournemouth.ac.uk

17

18

19

20

21

22

23

24

25 **Abstract**

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

41 **Introduction**

42 Through time, the areas inhabited by species are pushed and pulled in many directions by climate, habitat
43 changes, interactions with other species, and human transport. The latter has become a particularly
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
46 ranges. Not all species are equally successful when faced with such pressures. Identifying the key
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.

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

57 in or near human-impacted habitats, and it is frequently generalist species that capitalise on these
58 disturbed habitats and make good invaders (Marvier, Kareiva & Neubert, 2004). While much of the
59 available literature focuses on terrestrial endotherms and their adaptability in the face of human dominated
60 landscapes, comparatively little focuses on ectotherms – particularly snakes (Liu et al., 2020). This is
61 despite several prominent examples of introduced snakes (albeit in more natural landscapes) having
62 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,
64 1768)) are a constricting species in the family Colubridae. Native to mainland Europe, they range from
65 France in the West to Iran in the East (Musilová, Zavadil & Kotlík, 2007). The species previously
66 occupied a larger part of Northern Europe, only recently going extinct in Denmark during the early 1900s
67 (Allentoft, Rasmussen & Kristensen, 2018), with remaining relict populations in Germany, Switzerland,
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
102 represent pathways to mobile snakes, allowing us to infer their likely routes should this population spread
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
112 Mountain Zoo covering an area of 0.15 km². The Zoo grounds are highly disturbed because of the constant
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
118 throughout, with busy roads surrounding the zoo and the connecting meadows and pastures, with a dual
119 carriageway (A55) at the site's northernmost extremity.

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

122 13 males and eight females. Snakes were caught by hand, either during dedicated surveys,
123 opportunistically, during radio-tracking activities, or following notification by members of the public.
124 Two tracked individuals were caught by keepers at the Welsh Mountain Zoo during their daily activities.
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
130 implantation procedures ($n = 21$ implantations, mean = 7.34 ± 6.7 days held, range = 1 – 23 days). Snakes
131 were held in 70L plastic boxes (710 x 545 x 190 mm) in a temperature-controlled room at 21°C with
132 suitable refuge and water provided *ad libitum*.

133 Depending on their size, snakes were implanted with 1.2, 1.4 or 1.6 g Holohil BD-2T radio transmitters
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
138 capture in dry conditions warmer than 14°C. The only exception was M180 who was caught basking on
139 top of a hedge in a residential garden. The homeowner requested we release the snake a short distance
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**

144 We employed two different tracking regimes. In order to assess longer distance movements and home
145 range sizes, snakes were located twice daily as part of two daily tracking rounds, the first beginning at
146 10:00 and a second at 14:00. As we were a small team tracking many snakes, the timings of the tracks
147 were not precise, but animals were usually tracked once in the morning and once in the afternoon, and
148 almost always twice daily. See supplementary material for tracking periods and time lags.

149 In 2022 a subset of seven male snakes were located five times daily in order to determine what type of
150 habitat the snakes use when they are moving, with the greater tracking frequency allowing us to capture
151 more points in the movement pathway. These snakes were tracked in sessions beginning at 0900, 1100,
152 1300, 1500 and 1700. One female (F203) was tracked five times daily between 14/05/2022 and
153 14/06/2022, before switching to twice daily. After 20/08/2022, we began tracking the four male snakes
154 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
162 stochastic process movement models to our snake movement data. We first checked individuals for range
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
165 demonstrate range-residency from the home range analysis. We fitted multiple movement models and
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
171 (Calabrese, Fleming & Gurarie, 2016). For optimal performance we estimated autocorrelation and
172 covariance bias using perturbative hybrid residual maximum likelihood (pHREML), accounting for both
173 small absolute sample size and small effective sample size (Fleming et al., 2019). Absolute sample size
174 refers to the total number of times the animal was located during the tracking period, while effective
175 sample size is the entire tracking duration divided by how long it takes, on average, for the animal to cross
176 its linear home range. We then fit AKDEs using the guidance provided by Silva et al., (2022). We used
177 weighted AKDEc and pHREML to estimate home range size, which reduces oversmoothing of range
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

187 estimators, these models use animal locations over time to interpolate where animals might have been
188 during a tracking period, rather than extrapolating to their entire range (Alston et al., 2022b). However,
189 dBBMMs have utility in estimating space use during the study period, and allow for comparison with
190 other studies, giving a valuable impression of snake spatial ecology during the study period. As many
191 snakes were unlikely to have sufficient tracking durations to facilitate home range estimation, we use
192 estimates of space use derived from dBBMMs.

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

200 **Habitat selection**

201 All analyses were conducted using R v4.2.1 (R Core Team, 2022). For all habitat use analyses, we used
202 custom shape files of habitat types created in QGIS Using modified code from Smith et al (Smith et al.,
203 2021) and Hodges et al (Hodges et al., 2022), we converted our raster layers into layers with continuous
204 gradients denoting the Euclidean distance to habitat features. These layers were then inverted to avoid
205 zero-inflation and to ensure that the resulting outputs were easy to interpret, as positive values indicate
206 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.

218 **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
226 *INLA* package v22.05.07 (Rue, Martino & Chopin, 2009) we ran a population-level ISSF to ascertain
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 single-
231 factor models, one for each habitat type, and all models included the interaction of turn angle and step
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*
235 package v22.05.07 (Rue, Martino & Chopin, 2009), we used nested Laplace approximations in fitting
236 these models.

237 For the male snakes tracked five times daily, we ran both individual ISSFs as well as the “population-level
238 ISSFs” described above to investigate whether Aesculapian snakes demonstrated attraction to or
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 < 2
247 greater than the lowest were considered to have the largest influence.

248 **Seasonality and shelter locations**

249 We used two measures to determine seasonal behaviour changes in Aesculapian snakes, mean daily
250 displacement and dBBMM-derived motion variance (Hodges et al., 2022). We use dBBMMs to visualise
251 the space use of tracked snakes over the tracking period and ascertain areas of high use and re-use that are
252 of particular significance to Aesculapian snakes. We also use the estimates of motion variance they
253 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
258 confidence in the MDD estimates (see electronic supplementary material). To investigate seasonality, we
259 filtered the first and third daily tracks of snakes which received five tracks per day to allow comparison
260 between all individuals. We summed the movement distance across these two daily tracks to create our
261 values for daily displacement. We opportunistically collected observational data on the breeding
262 behaviour of this population during tracking activities, which allowed us to better inform the dates of the
263 mating and egg-laying seasons.

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

271 **Limitations and data statement**

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

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

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

283 **Results**

284 **Movements**

285 We tracked 13 adult male and eight adult female Aesculapian snakes between June and October 2021 and
286 May and September 2022. The average tracking duration was $56.67 \pm \text{SE } 7.85$ days (range 4 – 126 days).
287 We collected a total of 3232 snake locations, which included 947 relocations (a move from the previous
288 location). The mean daily displacement (MDD) for six male snakes on the twice daily tracking regime was
289 38.45 ± 21.33 m, and for the seven males on the five times daily regime it was 52.34 ± 26.43 m. The
290 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 asymptote (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
300 resident females was 23.32 ± 29.74 ha (range 0.28 – 65.31 ha). For eight range resident males it was 28.86
301 ± 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
303 effective sample sizes of six and 4.3 respectively, with pHREML bias in the order of 3% or higher (Table
304 1), and we applied parametric bootstrapping to these individuals. All models reflected elliptical home
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).

308 Table 1: Results of the snake AKDE home range analysis. Effective sample size refers to the number of
309 times the animal crossed its home range during the tracking period, while absolute sample size is the total
310 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 sample size	Absolute sample size	95% AKDE lower CI (ha)	95% AKDE estimate (ha)	95% AKDE upper CI (ha)	pHREML bias	Parametric bootstrap bias
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

315 **Fig 1. AKDE home ranges for tracked snakes that demonstrated range-residency.** A-D) Male snakes.
 316 E, F) Female snakes. Darkest shading in the centre represents the lower confidence interval for the 95%
 317 home range contour, medium shading is the 95% contour, and the lightest shading is the upper confidence
 318 interval. Points represent location data of each animal. While F203 did not demonstrate range residency,
 319 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

322 We estimated space use using dBBMMs (Table 2). We excluded three snakes with tracking durations less
 323 than 14 days (F212, F219, and M073) from the following means as their space use estimates would likely
 324 skew the results. For females, the mean area of the 95% confidence occurrence distributions was $2.09 \pm$
 325 3.79 ha (range = 0.02 – 10.51 ha). The mean area of the 95% confidence occurrence distributions for
 326 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.**

ID	90% (ha)	95% (ha)	99% (ha)	Tracking duration (days)	Total distance moved (m)	MDD (m)	Maximum daily distance (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**

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

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

342

343

344 **Fig 2. Coefficients from the weighted AKDE habitat selection functions for range resident snakes.**

345 Each plot displays the habitat selection of one individual snake. Positive values indicate selection for a
346 habitat type, while negative values indicate avoidance. Error bars represent 95% confidence intervals.

347 **ISSF at the population scale**

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

353

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

357 **Step length from five times daily tracking**

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

362 We also determined which features influenced the habitat selection of snakes. The top model was pasture
363 for M218. Gardens were top or second for M154 and M217. Hedgerows were top or second for M154 and
364 M209, while M207. M031, M154, and M202 were influenced by buildings (see electronic supplementary
365 material). Model selection results do not necessarily equate to definite selection or avoidance, however. At
366 the individual level, two snakes, M154 and M202, preferred to be closer to meadows and pasture. M218
367 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).

372

373

374 **Fig 4. Individual integrated step selection functions demonstrating the interaction between step**
375 **length and habitat types for Aesculapian snakes under the five times daily tracking regime.** Positive
376 values indicate longer steps associated with a habitat feature, and negative values indicate shorter steps.
377 Error bars indicate 95% confidence intervals. Circles indicate the features which were included in models
378 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-laying season from July to
381 mid August (Fig 5). The mean daily displacement (MDD) of females during the egg-laying season was
382 34.05 ± 75.45 m/day compared to 12.52 ± 32.33 m/day during the rest of the year (Fig 6). Across all
383 females there was only one day where an individual moved > 100 m outside of the egg-laying season, and
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
389 clutch of eggs inside this pile in 2019, confirming that it is an egg-laying site for the species. One further
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

393 **Fig 5. Motion variance plot for females and males through the study periods in 2021 and 2022.** Peaks
394 represent increased movement distances.

395

396 **Fig 6. Raincloud plot visualising the mean daily displacement of eight tracked female Aesculapian**
397 **snakes and 13 tracked male Aesculapian snakes through 2021-2022.** Each point represents the distance
398 moved by a snake on an individual day. Non-moves are excluded from the box and density plots, with

399 numbers inside the box showing the number of moving days in each season. Days without movement are
400 plotted to the far left along with a count. Mean daily displacement for each season, with non-moves
401 included, are printed along with a small black arrow. The egg-laying season (July 1st – August 16th) and
402 the mating season (15th May – 30th June) are compared with the rest of the active season for females and
403 males respectively. Fig created using code adapted from (Hodges et al., 2022).

404 The males showed a visible peak in motion variance the mating season between mid May and the end of
405 June (Fig 5). The MDD of males during the mating season was 68.7 ± 112.22 m/day compared to $26.3 \pm$
406 58.39 m/day during the rest of the year (Fig 6). Males only moved distances > 500 m per day during the
407 mating season, despite occasional periods of high activity in mid-summer. We observed one tracked male
408 mating on 13/06/2021 and another on 24/05/2022. We witnessed one of our tracked males in combat with
409 an unknown male on 15/06/2022. These observations reinforce our understanding of the timings of the
410 mating season of this species in Wales.

411 **Snake mortality**

412 Of our sample of 21 tracked snakes, five died during their tracking periods, and one died after tracking
413 was completed. In total, three females died. F177 was tracked during 2021 until the transmitter ran out of
414 battery, and was then found dead the following year on 15/08/2022 after a car strike (see supplementary
415 material). F142 was also killed by a car strike on 07/07/2021 after being tracked for 33 days, on the same
416 two-laned stretch of road as F177. Both snakes were gravid at the time of death, containing four and seven
417 well-developed eggs respectively. Lastly, F159 was cannibalised by a tracked male (M137) in August
418 2021 (Major et al., 2023).

419 Three of 13 male snakes died during the study. In 2021, M073 was predated by buzzards, with his
420 transmitter signal discovered in a pine tree containing a buzzard nest, approximately 30 m high up. M149
421 died from mammal predation. The snake was found at the edge of a meadow with approximately one
422 metre of trampled grass in all directions with a broken neck. Small sections of the snake had been
423 consumed. We suspect either a stoat, badger, or domestic cat was responsible. Finally, in the 2022 season,
424 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

430 who were repeatedly found in basking sites in vegetation at the edges of roads (M137 and M218). Females
431 selected a road verge (n = 1), compost or vegetation piles (n = 4), and buildings (n = 3) as repeated or
432 long-term shelter. Males chose a road verge (n = 1), compost or vegetation pile (n = 1), or buildings (n =
433 10). Five males used two different buildings for shelter, while three males used three different buildings.
434 These shelter sites were often used for long periods, and seven males and seven females spent ≥ 10 days in
435 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
439 preference for buildings in their introduced range in North Wales, with seven of eight individuals in our
440 AKDE-weighted habitat selection function selecting buildings as habitat, and our population SSF model
441 highlighted their importance to male snakes. Like many introduced species, Aesculapian snakes were
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-laying 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
448 for female snakes. Females spent long periods inactive during the **Spring** and early summer, remaining in
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,
458 2008; Reading and Jofré, 2009; Löwenborg et al., 2010). With urbanisation continuing unabated, the
459 ability to survive in human-dominated landscapes is valuable to individual species and vital for
460 maintaining biodiversity (Collins, Magle & Gallo, 2021). Herpetofauna and invertebrates remain
461 understudied in this realm, and our suite of analytical approaches represents an unusually detailed
462 investigation into the lives of a cryptic reptile species.

463 Our evidence here suggests that, like other snakes, Aesculapian snakes have peaks in activity due to their
464 reproductive cycles (Row, Blouin-Demers & Loughheed, 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
472 mortalities can be high for juvenile Aesculapian snakes (Kovar et al., 2014), and our study site lacks any
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
477 to increase their movement distances in highly disturbed areas, despite keeping smaller home ranges
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

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

498

499 **Acknowledgements**

500 We are indebted to the staff of the Welsh Mountain Zoo for their tireless support and assistance. Thank
501 you also to the generous residents of Colwyn Bay who allowed us to conduct fieldwork on their properties
502 with enthusiasm. We thank Henry Crisp, Jack Pearce, Gem Shinasi, and Andrea Pozzi for volunteering
503 their time to radio-track snakes. Thank you to Becca Snell for assisting with radio transmitter
504 implantations.

505 **References**

- 506 Allentoft ME, Rasmussen AR, Kristensen HV. 2018. Centuries-old DNA from an extinct population of
507 aesculapian snake (*zamenis longissimus*) offers new phylogeographic insight. *Diversity* 10. DOI:
508 10.3390/D10010014.
- 509 Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, Reineking B, Calabrese JM. 2022a.
510 Mitigating pseudoreplication and bias in resource selection functions with
511 autocorrelation-informed weighting. *Methods in Ecology and Evolution*:2041–210X.14025. DOI:
512 10.1111/2041-210X.14025.
- 513 Alston JM, Fleming CH, Noonan MJ, Tucker MA, Silva I, Folta C, Akre TSB, Ali AH, Belant JL, Beyer
514 D, Blaum N, Böhning-Gaese K, de Paula RC, Dekker J, Drescher-Lehman J, Farwig N, Fichtel C,
515 Fischer C, Ford AT, Janssen R, Jeltsch F, Kappeler PM, LaPoint SD, Markham AC, Medici EP,
516 Morato RG, Nathan R, Olson KA, Patterson BD, Petroelje TR, Ramalho EE, Rösner S, Oliveira
517 Santos LG, Schabo DG, Selva N, Sergiel A, Spiegel O, Ullmann W, Zieba F, Zwijacz-Kozica T,
518 Wittemyer G, Fagan WF, Müller T, Calabrese JM. 2022b. Clarifying space use concepts in
519 ecology: range vs. occurrence distributions. DOI: 10.1101/2022.09.29.509951.
- 520 Alworth LC, Hernandez SM, Divers SJ. 2011. Laboratory reptile surgery: principles and techniques.
521 *Journal of the American Association for Laboratory Animal Science* 50:11–26.
- 522 Andersen GE, Johnson CN, Barmuta LA, Jones ME. 2017. Use of anthropogenic linear features by two
523 medium-sized carnivores in reserved and agricultural landscapes. *Scientific Reports* 7:11624.
524 DOI: 10.1038/s41598-017-11454-z.

525 Ashton NM, Bowen DQ, Holman JA, Hunt CO, Irving BG, Kemp RA, Lewis SG, McNabb J, Parfitt S,
526 Seddon MB. 1994. Excavations at the Lower Palaeolithic site at East Farm, Barnham, Suffolk
527 1989-92. *Journal of the Geological Society* 151:599–605. DOI: 10.1144/gsjgs.151.4.0599.

528 Bartoszek IA, Smith BJ, Reed RN, Hart KM. 2021. Spatial ecology of invasive Burmese pythons in
529 southwestern Florida. *Ecosphere* 12. DOI: 10.1002/ecs2.3564.

530 Bauder JM, Peterman WE, Spear SF, Jenkins CL, Whiteley AR, McGarigal K. 2021. Multiscale
531 assessment of functional connectivity: Landscape genetics of eastern indigo snakes in an
532 anthropogenically fragmented landscape in central Florida. *Molecular Ecology* 30:3422–3438.
533 DOI: 10.1111/mec.15979.

534 Bielen A, Bošnjak I, Sepčić K, Jaklič M, Cvitanić M, Lušić J, Lajtner J, Simčič T, Hudina S. 2016.
535 Differences in tolerance to anthropogenic stress between invasive and native bivalves. *Science of*
536 *The Total Environment* 543:449–459. DOI: 10.1016/j.scitotenv.2015.11.049.

537 Bracis C, Bildstein KL, Mueller T. 2018. Revisitation analysis uncovers spatio-temporal patterns in
538 animal movement data. *Ecography*:1–11. DOI: 10.1111/ecog.03618.

539 Bubb DH, Lucas MC, Thom TJ. 2002. Winter movements and activity of signal crayfish *Pacifastacus*
540 *leniusculus* in an upland river, determined by radio telemetry. In: Thorstad EB, Fleming IA,
541 Næsje TF eds. *Aquatic Telemetry*. Dordrecht: Springer Netherlands, 111–119. DOI: 10.1007/978-
542 94-017-0771-8_13.

543 Calabrese JM, Fleming CH, Gurarie E. 2016. ctmm: An R package for analyzing animal relocation data as
544 a continuous-time stochastic process. *Methods in Ecology and Evolution* 7:1124–1132. DOI:
545 10.1111/2041-210X.12559.

546 Collins MK, Magle SB, Gallo T. 2021. Global trends in urban wildlife ecology and conservation.
547 *Biological Conservation* 261:109236. DOI: 10.1016/j.biocon.2021.109236.

548 Doherty TS, Hays GC, Driscoll DA. 2021. Human disturbance causes widespread disruption of animal
549 movement. *Nature Ecology & Evolution* 5:513–519. DOI: 10.1038/s41559-020-01380-1.

550 Dorcas ME, Willson JD, Reed RN, Snow RW, Rochford MR, Miller MA, Meshaka WE, Andreadis PT,
551 Mazzotti FJ, Romagosa CM, Hart KM. 2012. Severe mammal declines coincide with proliferation
552 of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy*
553 *of Sciences* 109:2418–2422. DOI: 10.1073/pnas.1115226109.

554 D'souza A, Gale GA, Marshall BM, Khamcha D, Waengsothorn S, Strine CT. 2021. Space use and
555 activity of *Boiga cyanea* – A major songbird nest predator in a seasonal tropical forest in
556 Thailand. *Global Ecology and Conservation* 32:e01875. DOI: 10.1016/j.gecco.2021.e01875.

557 Fieberg J, Signer J, Smith B, Avgar T. 2021. A 'How to' guide for interpreting parameters in
558 habitat-selection analyses. *Journal of Animal Ecology* 90:1027–1043. DOI: 10.1111/1365-
559 2656.13441.

560 Fleming CH, Calabrese JM. 2021. ctmm: continuous-time movement modeling.

561 Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. 2014. From Fine-Scale
562 Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes across
563 Spatiotemporal Scales. *The American Naturalist* 183:E154–E167. DOI: 10.1086/675504.

564 Fleming CH, Noonan MJ, Medici EP, Calabrese JM. 2019. Overcoming the challenge of small effective
565 sample sizes in home-range estimation. *Methods in Ecology and Evolution* 10:1679–1689. DOI:
566 10.1111/2041-210X.13270.

567 Hanslowe EB, Falk BG, Collier MAM, Josimovich JM, Rahill TA, Reed RN. 2016. First Record of
568 Invasive Burmese Python Oviposition and Brooding Inside an Anthropogenic Structure.
569 *Southeastern Naturalist* 15:103–106.

570 Hawley Matlaga TJ, Burrowes PA, Hernández-Pacheco R, Pena J, Sutherland C, Wood TE. 2021.
571 Warming increases activity in the common tropical frog *Eleutherodactylus coqui*. *Climate Change*
572 *Ecology* 2:100041. DOI: 10.1016/j.ecochg.2021.100041.

573 Hiley JR, Bradbury RB, Holling M, Thomas CD. 2013. Protected areas act as establishment centres for
574 species colonizing the UK. *Proceedings of the Royal Society B: Biological Sciences*
575 280:20122310. DOI: 10.1098/rspb.2012.2310.

576 Hodges CW, Marshall BM, Iii JGH, Strine CT. 2022. Malayan kraits (*Bungarus candidus*) show affinity
577 to anthropogenic structures in a human dominated landscape. *Scientific Reports* 12:7139.

578 Jones MD, Marshall BM, Smith SN, Crane M, Silva I, Artchawakom T, Suwanwaree P, Waengsothorn S,
579 Wüster W, Goode M, Strine CT. 2022. How do King Cobras move across a major highway?
580 Unintentional wildlife crossing structures may facilitate movement. *Ecology and Evolution*
581 12:e8691. DOI: 10.1002/ece3.8691.

582 Kays R, Davidson SC, Berger M, Bohrer G, Fiedler W, Flack A, Hirt J, Hahn C, Gauggel D, Russell B,
583 Kölzsch A, Lohr A, Partecke J, Quetting M, Safi K, Scharf A, Schneider G, Lang I, Schaeuffelhut
584 F, Landwehr M, Storhas M, van Schalkwyk L, Vinciguerra C, Weinzierl R, Wikelski M. 2022.
585 The Movebank system for studying global animal movement and demography. *Methods in*
586 *Ecology and Evolution* 13:419–431. DOI: 10.1111/2041-210X.13767.

587 Keller WL, Heske EJ. 2000. Habitat Use by Three Species of Snakes at the Middle Fork Fish and Wildlife
588 Area, Illinois. *Journal of Herpetology* 34:558–564. DOI: 10.2307/1565271.

589 Kovar R, Brabec M, Vita R, Bocek R. 2014. Mortality Rate and Activity Patterns of an Aesculapian Snake
590 (*Zamenis longissimus*) Population Divided by a Busy Road. *Journal of Herpetology* 48:24–33.
591 DOI: 10.1670/12-090.

592 Kranstaber B, Smolla M, Scharf AK. 2022. move: Visualizing and Analyzing Animal Track Data.

593 Lelièvre H, Blouin-Demers G, Bonnet X, Lourdais O. 2010. Thermal benefits of artificial shelters in
594 snakes: A radiotelemetric study of two sympatric colubrids. *Journal of Thermal Biology* 35:324–
595 331. DOI: 10.1016/j.jtherbio.2010.06.011.

596 Lenoir J, Svenning J-C. 2015. Climate-related range shifts – a global multidimensional synthesis and new
597 research directions. *Ecography* 38:15–28. DOI: 10.1111/ecog.00967.

598 Liu C, Wolter C, Xian W, Jeschke JM. 2020. Most invasive species largely conserve their climatic niche.
599 *Proceedings of the National Academy of Sciences* 117:23643–23651. DOI:
600 10.1073/pnas.2004289117.

601 Major T, Bracegirdle R, Gandini A, Russell GL, Pozzi AV, Morgan R, Mulley JF, Wüster W. 2023. Mate
602 today, gone tomorrow: male-on-female cannibalism in *Zamenis longissimus* (Laurenti, 1768) in
603 North Wales. *Herpetology Notes* 16:51–54.

604 Marshall BM, Crane M, Silva I, Strine CT, Jones MD, Hodges CW, Suwanwaree P, Artchawakom T,
605 Waengsothorn S, Goode M. 2020. No room to roam: King Cobras reduce movement in
606 agriculture. *Movement Ecology* 8:1–14. DOI: 10.1186/s40462-020-00219-5.

607 Marvier M, Kareiva P, Neubert MG. 2004. Habitat Destruction, Fragmentation, and Disturbance Promote
608 Invasion by Habitat Generalists in a Multispecies Metapopulation. *Risk Analysis* 24:869–878.
609 DOI: 10.1111/j.0272-4332.2004.00485.x.

610 Mitchell TS, Folt B, Hall JM. 2021. Dumpsters and other anthropogenic structures as habitat for invasive
611 African rock agama lizards in Florida. *Biological Invasions* 23:2689–2693. DOI: 10.1007/s10530-
612 021-02537-0.

613 Moyle PB, Marchetti MP. 2006. Predicting Invasion Success: Freshwater Fishes in California as a Model.
614 *BioScience* 56:515–524. DOI: 10.1641/0006-3568(2006)56[515:PISFFI]2.0.CO;2.

615 Muff S, Signer J, Fieberg J. 2019. Accounting for individual-specific variation in habitat-selection studies:
616 Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal*
617 *of Animal Ecology* 89:80–92. DOI: 10.1111/1365-2656.13087.

618 Musilová R, Zavadil V, Kotlík P. 2007. Isolated populations of *Zamenis longissimus* (Reptilia: Squamata)
619 above the northern limit of the continuous range in Europe: origin and conservation status. *Acta*
620 *Societatis Zoologicae Bohemicae* 71:197–208.

621 QGIS Development Team. 2023. QGIS Geographic Information System. Open Source Geospatial
622 Foundation Project.

623 R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical
624 Computing, Vienna, Austria.

625 Reinert HK, Cundall D. 1982. An improved surgical implantation method for radio-tracking snakes.
626 *Copeia* 1982:702–705. DOI: 10.2307/1444674.

627 Rickart EA, Balete DS, Rowe RJ, Heaney LR. 2011. Mammals of the northern Philippines: tolerance for
628 habitat disturbance and resistance to invasive species in an endemic insular fauna. *Diversity and*
629 *Distributions* 17:530–541. DOI: 10.1111/j.1472-4642.2011.00758.x.

630 Rodda GH, Savidge J a. 2007. Biology and Impacts of Pacific Island Invasive Species. 2. **Boiga**
631 **irregularis**, the Brown Tree Snake (Reptilia: Colubridae)1. *Pacific Science* 61:307–324. DOI:
632 10.2984/1534-6188(2007)61[307:BAIOPI]2.0.CO;2.

633 Roe JH, Gibson J, Kingsbury BA. 2006. Beyond the wetland border: Estimating the impact of roads for
634 two species of water snakes. *Biological Conservation* 130:161–168. DOI:
635 10.1016/j.biocon.2005.12.010.

636 Row JR, Blouin-Demers G, Lougheed SC. 2012. Movements and habitat use of Eastern Foxsnakes
637 (**Pantherophis gloydi**) in two areas varying in size and fragmentation. *Journal of Herpetology*
638 46:94–99. DOI: 10.1670/10-262.

639 Rowcliffe JM, Carbone C, Kays R, Kranstauber B, Jansen PA. 2012. Bias in estimating animal travel
640 distance: the effect of sampling frequency. *Methods in Ecology and Evolution* 3:653–662. DOI:
641 10.1111/j.2041-210X.2012.00197.x.

642 Rue H, Martino S, Chopin N. 2009. Approximate Bayesian Inference for Latent Gaussian models by using
643 Integrated Nested Laplace Approximations. *Journal of the Royal Statistical Society Series B:*
644 *Statistical Methodology* 71:319–392. DOI: 10.1111/j.1467-9868.2008.00700.x.

645 Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing tracking data
646 and conducting habitat selection analyses. *Ecology and Evolution* 9:880–890. DOI:
647 10.1002/ece3.4823.

648 Silva I, Crane M, Marshall BM, Strine CT. 2020. Reptiles on the wrong track? Moving beyond traditional
649 estimators with dynamic Brownian Bridge Movement Models. *Movement Ecology* 8:1–13. DOI:
650 10.1186/s40462-020-00229-3.

651 Silva I, Crane M, Suwanwaree P, Strine C, Goode M. 2018. Using dynamic brownian bridge movement
652 models to identify home range size and movement patterns in king cobras. *PLoS ONE* 13:1–20.
653 DOI: 10.1371/journal.pone.0203449.

654 Silva I, Fleming CH, Noonan MJ, Alston J, Folta C, Fagan WF, Calabrese JM. 2022.
655 Autocorrelation-informed home range estimation: A review and practical guide. *Methods in*
656 *Ecology and Evolution* 13:534–544. DOI: 10.1111/2041-210X.13786.

657 Smith SN, Jones MD, Marshall BM, Waengsothorn S, Gale GA, Strine CT. 2021. Native Burmese
658 pythons exhibit site fidelity and preference for aquatic habitats in an agricultural mosaic. *Scientific*
659 *Reports* 11:1–13. DOI: 10.1038/s41598-021-86640-1.

660 de Solla SR, Bonduriansky R, Brooks RJ. 1999. Eliminating autocorrelation reduces biological relevance
661 of home range estimates. *Journal of Animal Ecology* 68:221–234. DOI: 10.1046/j.1365-
662 2656.1999.00279.x.

663 Sparks TH, Dennis RLH, Croxton PJ, Cade M. 2007. Increased migration of Lepidoptera linked to climate
664 change. *European Journal of Entomology* 104:139–143. DOI: 10.14411/eje.2007.019.

665 Thompson JJ, Morato RG, Niebuhr BB, Alegre VB, Oshima JEF, de Barros AE, Paviolo A, de la Torre
666 JA, Lima F, McBride RT, Cunha de Paula R, Cullen L, Silveira L, Kantek DLZ, Ramalho EE,
667 Maranhão L, Habermeld M, Sana DA, Medellín RA, Carrillo E, Montalvo VH, Monroy-Vilchis O,
668 Cruz P, Jacomo ATA, Alves GB, Cassaigne I, Thompson R, Sáenz-Bolaños C, Cruz JC, Alfaro
669 LD, Hagnauer I, Xavier da Silva M, Vogliotti A, Moraes MFD, Miyazaki SS, Araujo GR, Cruz da
670 Silva L, Leuzinger L, Carvalho MM, Rampim L, Sartorello L, Quigley H, Tortato FR,
671 Hoogesteijn R, Crawshaw PG, Devlin AL, May Júnior JA, Powell GVN, Tobler MW, Carrillo-
672 Percastegui SE, Payán E, Azevedo FCC, Concone HVB, Quiroga VA, Costa SA, Arrabal JP,
673 Vanderhoeven E, Di Blanco YE, Lopes AMC, Ribeiro MC. 2021. Environmental and
674 anthropogenic factors synergistically affect space use of jaguars. *Current Biology* 31:3457-
675 3466.e4. DOI: 10.1016/j.cub.2021.06.029.

676 Webster MM, Rutz C. 2020. How STRANGE are your study animals? *Nature* 582:337–340. DOI:
677 10.1038/d41586-020-01751-5.

678 Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis.

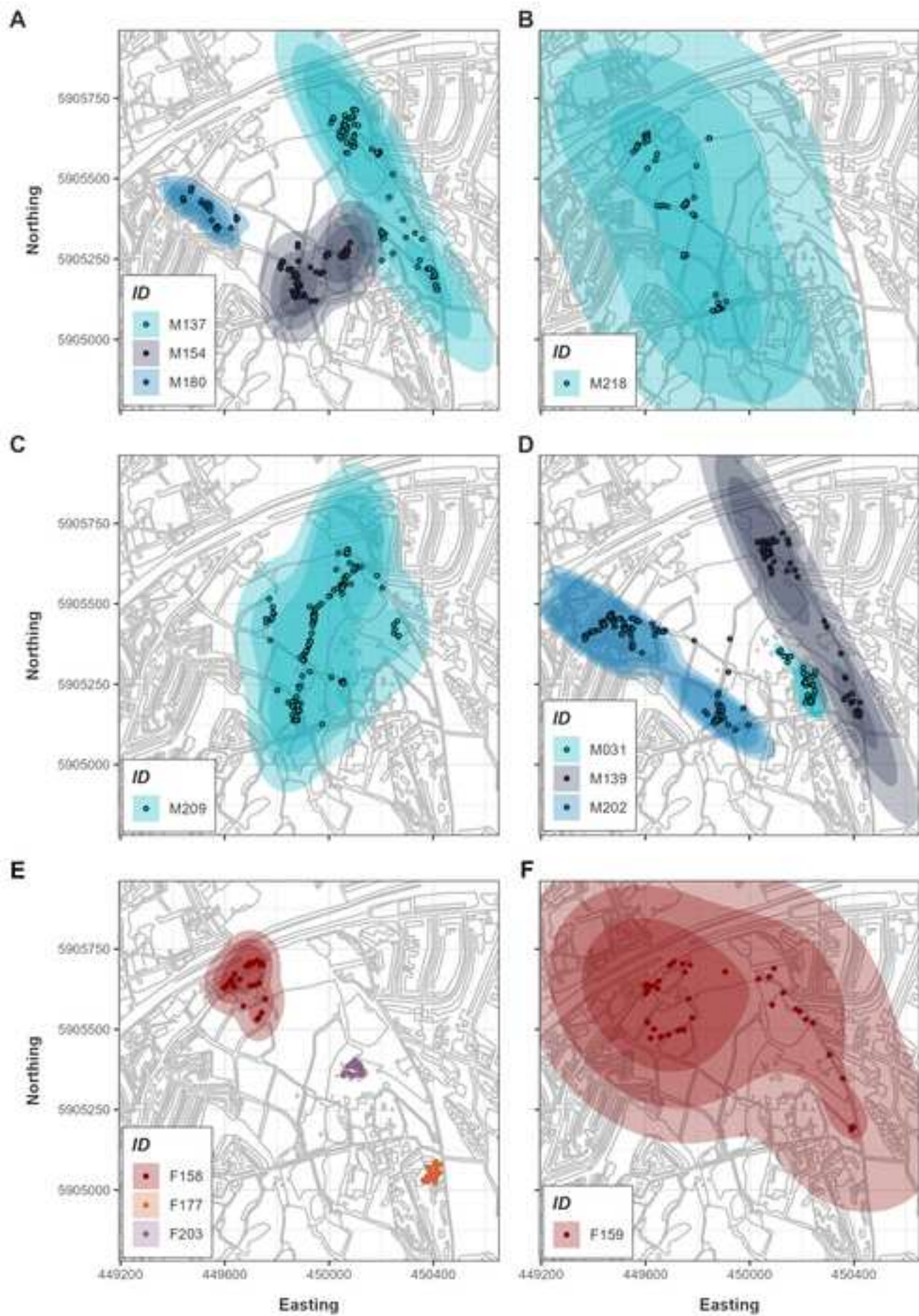
679 Wickham H, François R, Henry L, Müller K, Davis V. 2022. dplyr: A Grammar of Data Manipulation.

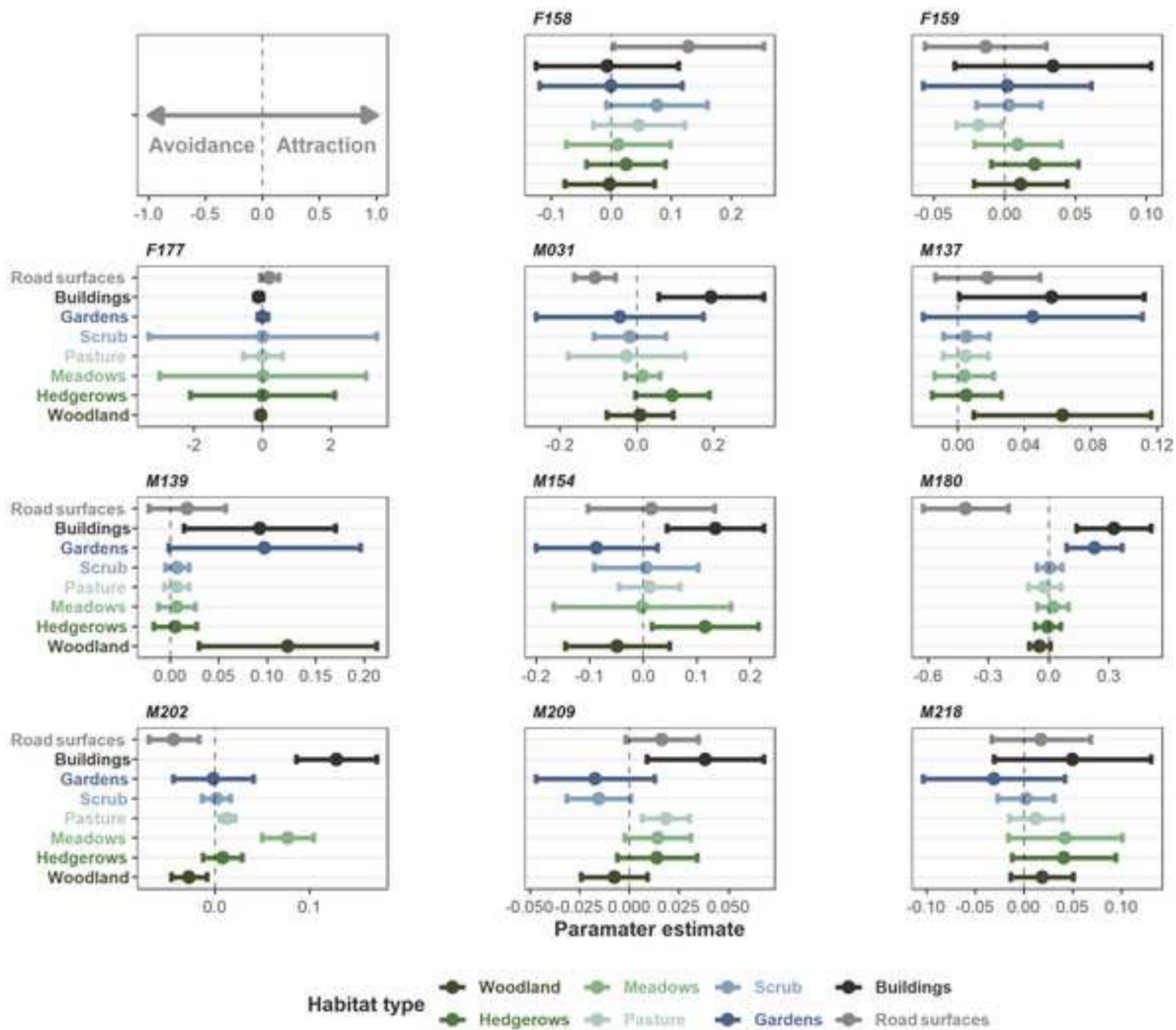
680 Yu X, Wu NC, Ge L, Li L, Zhang Z, Lei J. 2022. Artificial shelters provide suitable thermal habitat for a
681 cold-blooded animal. *Scientific Reports* 12:5879. DOI: 10.1038/s41598-022-09950-y.

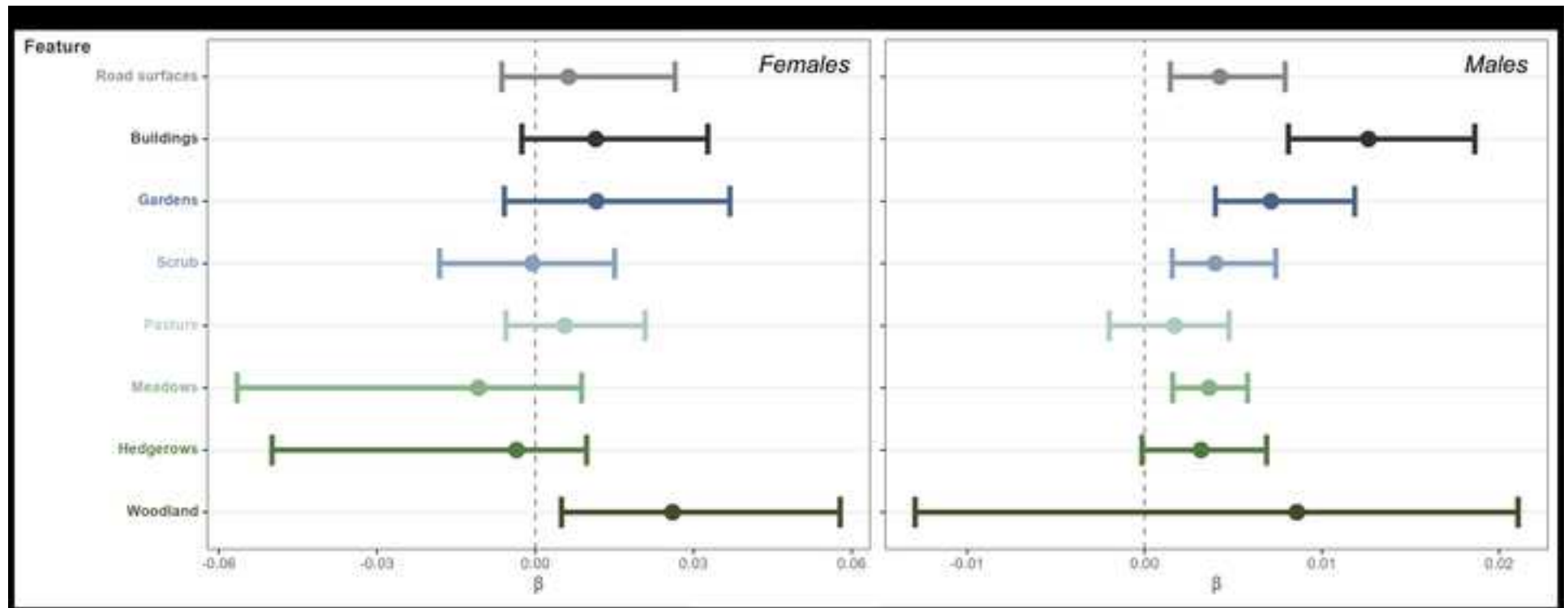
682

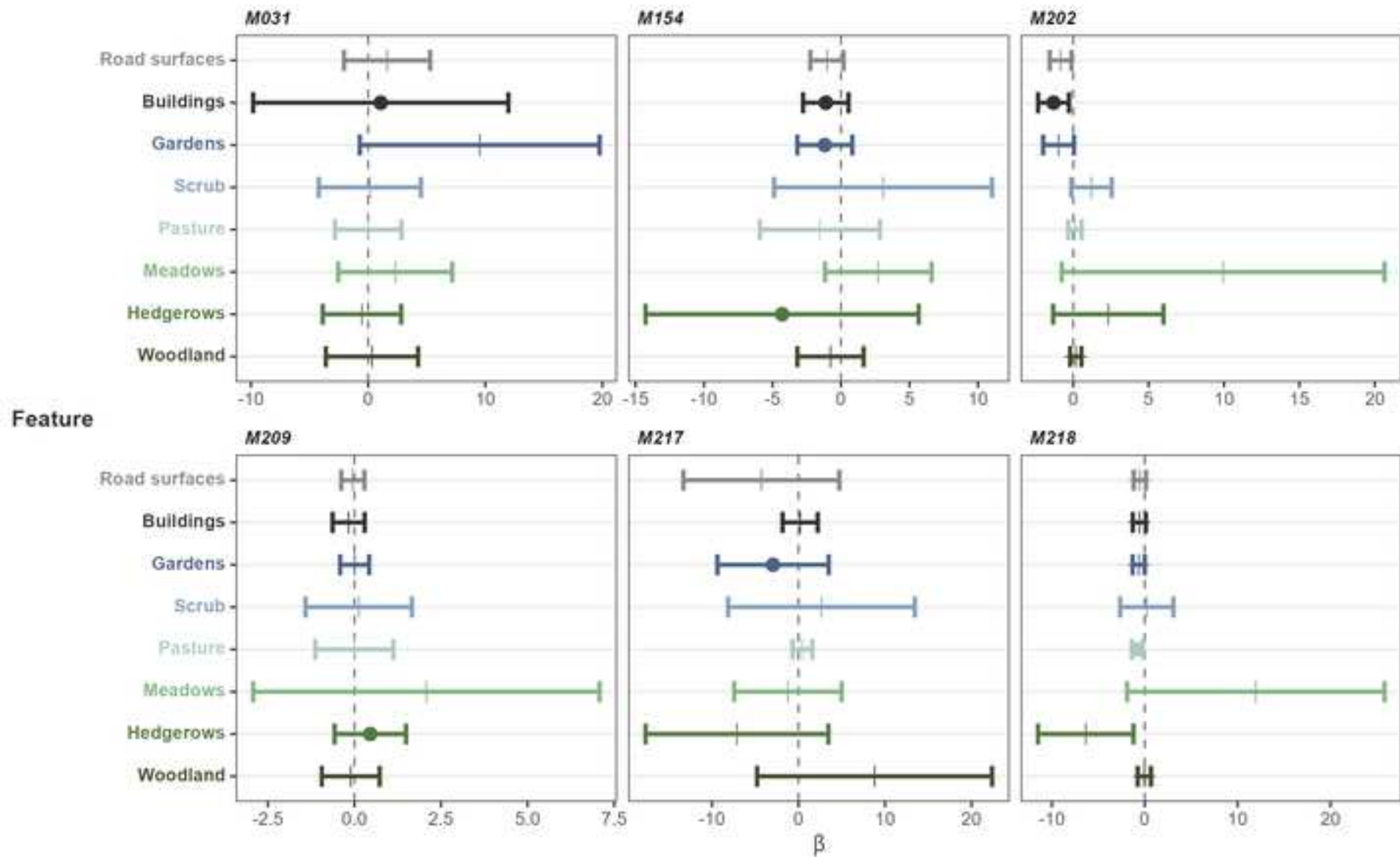
683

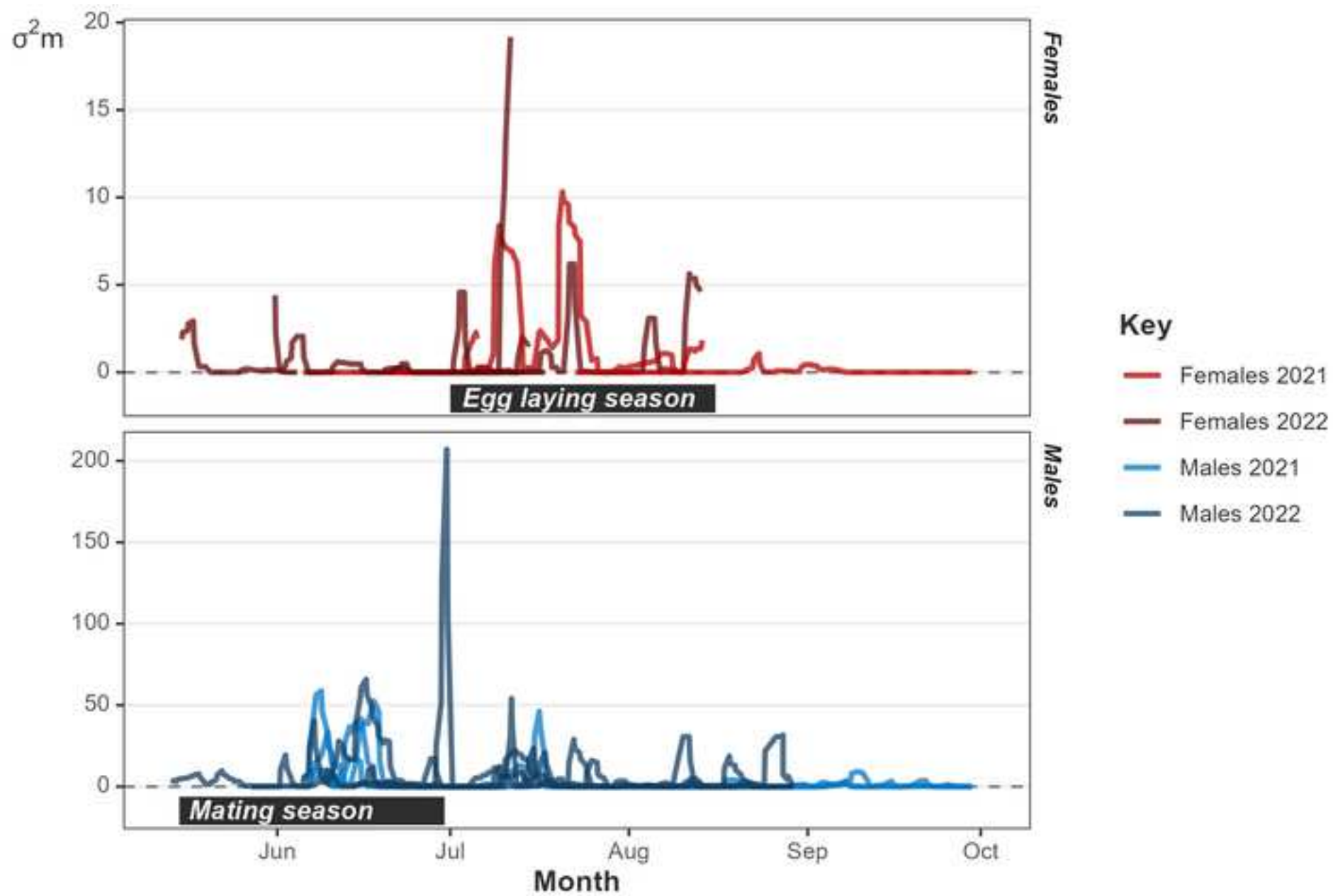
684

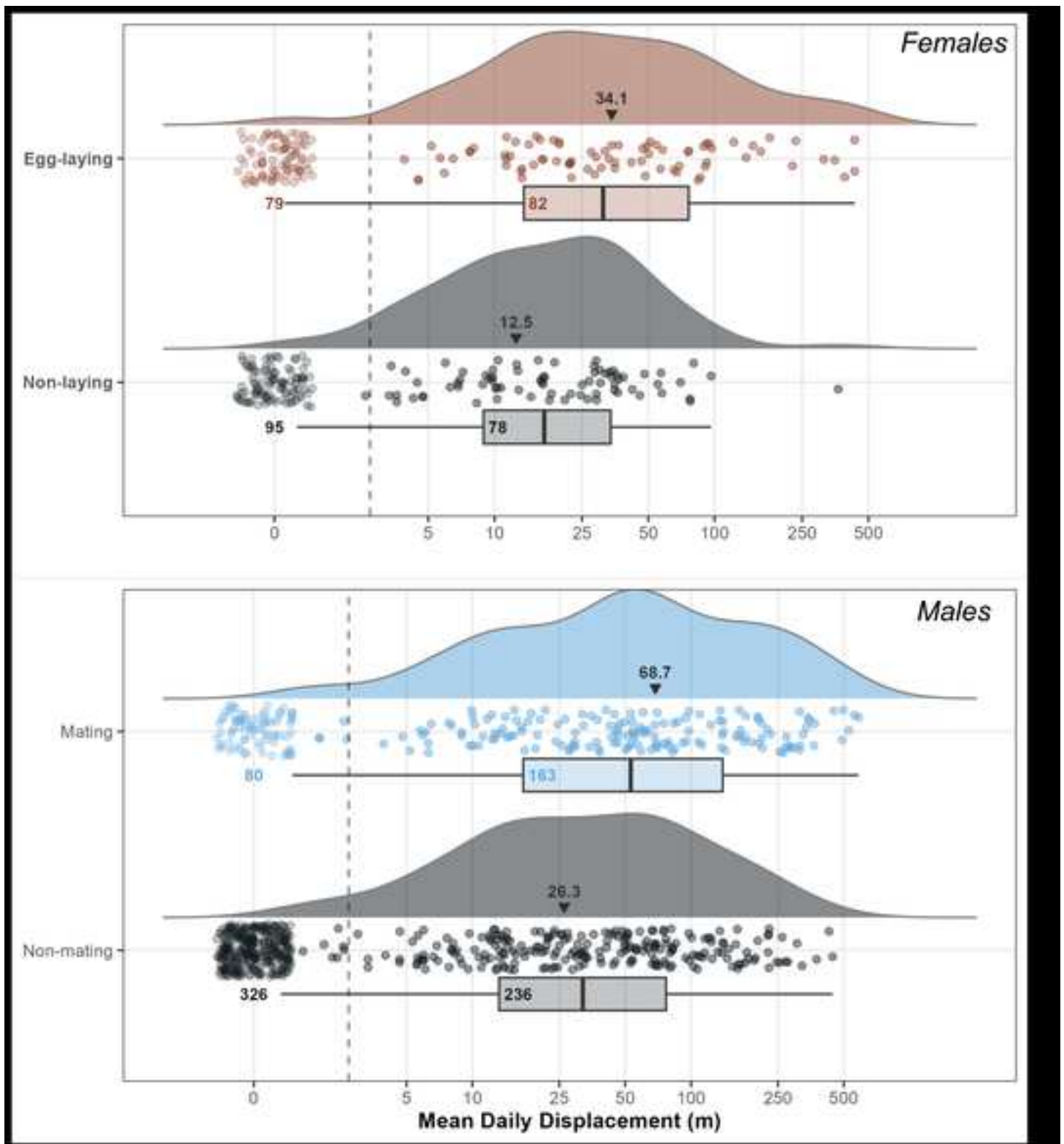














Click here to access/download
Supporting Information
Supplementary material.docx

