

1 **Title:** Spatial ecology of the Endangered and endemic Sagalla caecilian (*Boulengerula*  
2 *nieden*) in the Eastern Arc Mountains of Kenya

3

4 **Authors:** David Marquis, Basil Mashanga, Ben Tapley, Oliver Wearn, Olivia Couchman,  
5 Rikki Gumbs, Claudia Gray, and Marcus Rowcliffe

6

7 **Address:** ZSL, Regent's Park, London NW1 4RY, UK

8 Department of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY

9

10 **Keywords:** Gymnophiona, Herpelidae, soil ecology, amphibian conservation, Kenya,  
11 Taita Hills.

12

13 **Abstract**

14 Caecilians (Order Gymnophiona) are generalist predators of soil invertebrates, and may  
15 therefore play an important role in tropical soil ecosystems. However, their fossorial  
16 lifestyle and the associated difficulties in surveying them have caused a deficit in data  
17 for the majority of species. We applied a systematic approach and an intensive  
18 sampling strategy to an Endangered and evolutionarily distinct caecilian from the  
19 Eastern Arc Mountains, the Sagalla caecilian (*Boulengerula niedeni*). We investigated  
20 the association between habitat type and caecilian occupancy across its entire range,  
21 the Sagalla Hill, Kenya, and explored the relationship between several variables (land  
22 use type, surface soil temperature, soil compactness, and landowner prediction of  
23 caecilian presence) and its presence in different habitats. We found no significant

24 effects of any of the investigated variables in predicting caecilian presence across the  
25 Sagalla landscape. Instead, our findings suggest that the species survives at least as  
26 well in agricultural landscapes as it does in areas with indigenous vegetation with an  
27 estimated density of around 900 caecilians per hectare. A bimodal distribution of sizes  
28 and weights of captured specimens suggests ongoing successful breeding and  
29 recruitment. This suggests that there is a case for cautious optimism with regard to the  
30 status of *B.niederi*. Our work could act as a useful pilot for further, improved caecilian  
31 surveys in the Eastern Arc Mountains and beyond, to improve our understanding and  
32 conservation of these overlooked fossorial amphibians.

33 **Introduction**

34 Amphibian populations are undergoing global declines with as many as 42% of  
35 assessed species now threatened with extinction (Leudtke et al. 2023. Habitat  
36 deterioration, climate change, and disease are thought to be some of the leading  
37 causes of population declines (e.g., Pounds et al. 2006; Wake & Vredenburg, 2008,  
38 Scheele et al. 2019; Leudtke et al. 2023), however the vast majority of amphibian  
39 research has been biased towards anuran and caudate amphibians, with the lesser  
40 known third order, the legless, primarily soil dwelling Gymnophiona (commonly referred  
41 to as caecilians), receiving relatively little attention (e.g., Gower et al. 2005; de Oliveira  
42 Ferronato, 2019).

43         The subterranean lifestyle of many caecilians has precluded them from various  
44 biodiversity surveys, perpetuating the impression that they occur in low densities and  
45 have little impact on ecosystem function (Gower & Wilkinson, 2005; Decaëns et al.  
46 2006). However, some studies have found certain species of caecilian to be abundant in  
47 particular localities (e.g., Bhatta, 1997; Oommen et al. 2000; Measey, 2004; Kupfer et  
48 al. 2005), suggesting their impact on ecosystem function may be underestimated.  
49 Moreover, as generalist predators of soil ecosystem engineers (SEE), such as ants,  
50 termites, and earthworms (e.g., Measey et al. 2003; Gaborieau & Measey, 2004; Kupfer  
51 et al. 2005; Jones et al. 2006; Kouete & Blackburn 2020), locally abundant caecilians  
52 may exert some degree of regulation over SEE populations, further underscoring the  
53 need for greater research into these interactions (e.g., Measey et al. 2003).

54         Caecilians could also prove to be useful indicator species for soil ecosystems  
55 (Measey, 2006), particularly with the unpredictable effects that anthropogenic climate

56 change is likely to have on soil ecosystems worldwide (Copley, 2000; Decaëns et al.  
57 2006). With reports of several caecilian species being commonly encountered in low-  
58 intensity agricultural landscapes (Hebrard et al. 1992; Measey, 2004;; Jared et al. 2015;  
59 Malonza, 2016), these species could be indicators of soil degradation or pesticide  
60 toxicity, though this requires more investigation (Oommen et al. 2000; Gower &  
61 Wilkinson, 2005).

62         A contributing factor to the paucity of caecilian research is the challenge of  
63 surveying them. Soil is an opaque, dense, and heterogeneous medium that requires  
64 considerable energy and destructive force to sample comprehensively (Decaëns et al.  
65 2006; Measey, 2006). A basic component of caecilian surveys is manually excavating  
66 the soil, a labour-intensive process with a relatively low return in terms of the number of  
67 caecilians sighted per unit of effort expended, partly due to the often patchy yet poorly  
68 understood distribution of many caecilian species (Largen et al. 1972; Measey et al.  
69 2003; Gower & Wilkinson, 2005). This challenge has inhibited the development of  
70 effective tools for measuring ecological parameters for most caecilian species, though  
71 efforts by Measey (2006) to develop a standardised methodology have been a step in  
72 the right direction. This challenge has resulted in over half (97/193) of caecilian species  
73 being assessed as Data Deficient by the IUCN (IUCN, 2023), with few quantitative  
74 historical datasets against which to compare current populations (Measey et al. 2009).  
75 For this reason, statements on declines in caecilian species are often founded on recent  
76 surveys having returned no individuals from sites of known historical presence (Gower  
77 & Wilkinson, 2005 and references therein), or inferences made from broader soil  
78 herpetofaunal declines (Pooley et al. 1973; Measey et al. 2009).

79

80 The focal species for this study was the Sagalla caecilian (*Boulengerula niedeni*), an  
81 Endangered herpelid caecilian that is endemic to Sagalla Hill in south-eastern Kenya.  
82 Sagalla is located approximately 30 km east of the comparatively well-studied Taita  
83 Hills, and together they form the northernmost reach of the Eastern Arc Mountains, a  
84 global biodiversity hotspot (Myers et al. 2000; Malonza et al. 2010). Described in 2005  
85 (Müller et al. 2005), this species was previously seldom distinguished from earthworms  
86 (phylum Annelida) by the inhabitants of Sagalla, who generally consider it of little use or  
87 value, a known issue for East African caecilians (Loader et al. 2003). A naming contest  
88 held in 2006 was successful in raising awareness for the species, with the name *Kilima-*  
89 *mrota* eventually chosen, meaning “thin burrowing animal” in the KiSagalla language  
90 (Wojnowski & Malonza, 2009). The species is assessed as Endangered by the IUCN  
91 Red List (IUCN SSC, 2013) and recognised as a global priority for conservation on the  
92 basis of its evolutionary distinctiveness (Isaac et al. 2012; Gumbs et al. 2018). It has a  
93 species action plan (Nature Kenya, National Museums of Kenya, Kenya Wildlife Service  
94 & Kenya Forest Service, 2015) and may have benefited from targeted attempts to  
95 restore native habitat by planting indigenous trees and replacing exotic eucalyptus with  
96 indigenous trees (Malonza, 2016; IUCN SSC, 2013).

97 The objective of this study was to quantitatively assess the distribution and  
98 occupancy of *B. niedeni* across its distributional range, to better inform future  
99 conservation work aimed at protecting the biodiversity of Sagalla Hill. We sought to test  
100 if land use type was correlated with species’ occurrence across this heavily altered  
101 landscape. An ancillary objective was to collect data on environmental and soil

102 variables, to explore the species' preferred habitat conditions. To the best of our  
103 knowledge it is one of the most intensive sampling efforts of an African caecilian  
104 amphibian, and the first to sample at randomly selected sites across the entire range of  
105 a caecilian species.

106

## 107 **Methods**

### 108 *Ethics and Biosecurity statement*

109 This project was approved by the ethics committee of Imperial College London's  
110 Department of Life Sciences. All methods used in this study were non-invasive and did  
111 not require a UK Home Office Licence and were compliant with the BHS Ethics Policy  
112 (British Herpetological Society, 2017). Research was carried out under the Taita Taveta  
113 Wildlife Forum's research permits issued by the Kenya Wildlife Service and Kenya  
114 Forest Service. To reduce the risk of pathogen transmission between sites and  
115 individuals we disinfected all equipment between sites and all animals were handled  
116 with powder-free nitrile gloves which were changed between individuals. A euthanasia  
117 protocol was established in case of accidental injury of a caecilian during the digging  
118 process: individuals whose survival was judged to be unlikely (3 individuals) were  
119 immediately euthanised by the ventral application of 20% benzocaine cream (Orajel™)  
120 and preserved before being deposited at the National Museum of Kenya.

121

### 122 *Data collection*

123 Fieldwork was carried out on Sagalla Hill in south-eastern Kenya (3.499° S, 38.580° E,  
124 580–1450 metres above sea level) in May and June of 2016, in the transition season

125 between the long rains (March–May) and the cooler, dry winter (June–September).  
126 Caecilians were sought at pre-determined sites on a systematic grid covering the whole  
127 of Sagalla Hill, with the intent to produce data for occupancy modelling. Given that the  
128 semi-arid lowland habitat surrounding Sagalla represents a barrier to amphibian  
129 dispersal and that the nearby Taita Hills have been well sampled and only ever  
130 produced the closely related yet distinct Taita caecilian (*Boulengerula taitanus*; Malonza  
131 & Measey, 2005), we assumed that the entire range of *B. niedeni* was covered by this  
132 study. A three-person team visited 76 sites over 36 days, between the times of 0700  
133 and 1100 hrs to avoid the heat of mid-day. A total of 204.8 person hours were spent  
134 digging for caecilians. We estimated the total number of sites that could feasibly be  
135 visited within the planned research period and created a grid with this number of sites  
136 spaced evenly across the entire study area, resulting in a constant spacing of 400 m  
137 between sites (Fig. 1). This even spacing of sites ensured that all land use types were  
138 sampled roughly in proportion to their occurrence on the landscape. As it was highly  
139 unlikely that individual caecilians moved between sites within the duration of data  
140 collection, we assumed that the 400 m spacing between sites meant that each site  
141 could be considered as an independent sample. We allocated each site to one of three  
142 categories of land use (1) agricultural land, which includes active and fallow fields as  
143 well as areas dominated by fruiting trees, (2) heavily anthropogenically disturbed land,  
144 including urban centres, habitations, school compounds, and non-native pine and  
145 *Eucalyptus* plantations, and (3) natural, relatively undisturbed areas, including  
146 unmanaged shrubby or forested areas and the last remaining patch of Sagalla's  
147 indigenous forest. Given the small remaining area of the indigenous forest habitat, it

148 was over-sampled, with two sites added equidistantly between existing indigenous  
149 forest sites (i.e. 200 m apart) to increase the coverage of this habitat.

150 To find caecilians, a standardised search protocol was developed by the author  
151 (BT) with the input of David Gower and Mark Wilkinson (Natural History Museum,  
152 London). At each of the 76 sites, three 1.5 m x 1.5 m plots were dug, giving a total of  
153 228 plots. Digging used a systematic method, with two workers standing side by side  
154 and digging forward, to a targeted depth of 30 cm as . The depth of the excavated plot  
155 followed previous studies (Measey et al. 2003; Measey 2004). The digging tools used  
156 were local implements known as *jembes*, which consist of a metal blade (approx. 15 x  
157 15 cm) fixed roughly perpendicularly to a 1m long wooden handle, which is raised  
158 overhead and swung downwards. These tools have been widely used to excavate  
159 caecilians, including congeneric species (e.g. Malonza & Measey, 2005; Measey et al.  
160 2006; Measey et al. 2012).

161 Plots were dug as near as possible to the exact GPS marker at each site, with  
162 the intent to retain its randomness. However, it was not always possible to dig on the  
163 exact GPS location, either due to the terrain (boulders, dangerously steep gradient) or  
164 due to landowners withholding their consent for digging on their property, as was often  
165 the case with cultivated fields. In such cases, the first plot was dug as near as possible  
166 and never more than 10 m away from the GPS marker.

167 The second and third plot dug at each site were situated in perceived favourable  
168 caecilian microhabitat within 100 m of the GPS marker, with the exact locations selected  
169 according to the following criteria, in decreasing order of priority: 1) maximal apparent  
170 soil moisture, 2) proximity to banana plants, 3) proximity to fruiting trees, 4) maximal



171 apparent soil fertility/organic matter content (leaf piles, cow dung). These selection  
172 criteria were based on a review of previous caecilian surveys where favourable  
173 caecilian habitat had been described (e.g., Hebrard et al. 1992; Bhatta, 1997, Measey,  
174 2004; Gower & Wilkinson, 2005; Kupfer et al. 2005; Kouete & Blackburn 2000). In rare  
175 cases where none of these criteria could be met, the second and third plots were dug in  
176 effectively random microhabitat exactly 30 m east and west of the GPS marker.

177         After each plot was dug, a suite of environmental variables was recorded. Soil  
178 moisture, soil pH, and ambient light were measured with a Mudder 3-in-1  
179 Moisture/pH/Light meter. Soil temperature was measured using a ThermaPen (Electronic  
180 Temperature Instruments Ltd) inserted to a depth of 5 cm while the soil compaction was  
181 measured using a Humboldt H-4200 Soil Penetrometer on bare soil, with 3 replicates of  
182 each variable taken at the edge of each plot following the manufacturers guidelines and  
183 only after the plot had been excavated to prevent disturbing caecilians within the plot  
184 prior to excavation. (Table S1; see supplemental materials). Excavated material was  
185 carefully checked for the presence of caecilians. Captured caecilians were weighed with  
186 a Pesola LightLine Spring Scale, their total length measured to the nearest mm by  
187 placing the caecilian in a clear, Ziploc bag and manipulating the caecilian so that it lies  
188 straight along the inside edge of the bag where its total length was then measured with  
189 a haberdashery tape. Caecilians were released at the point of capture.

190         In addition to the 288 systematically distributed plots, a further exploratory 63  
191 plots were dug using the same protocol as above, but selected opportunistically, either  
192 at sites with known historical presence (from Malonza et al. 2010), or at sites in habitat  
193 expected to be favourable to caecilians based on prior information and experience

194 during the survey. These plots yielded additional specimens whose length and weight  
195 data added to the analysis of morphology.

196

#### 197 *Landowner survey*

198 In cases where the site fell on private land, a short standardised social survey was  
199 incorporated into conversation while seeking landowner permission to dig a plot on their  
200 property. All landowners spoken to were over 18 years of age, gave consent for data to  
201 be collected and used, and were informed of their right to withdraw their consent at any  
202 time. These conversations were carried out in the local KiSagalla language and three  
203 questions were asked: 1. Have you heard of the Sagalla caecilian? (identified by its  
204 KiSagalla name, *kilima-mrota*), 2. Do you recognise it from these images?, and 3. Have  
205 you ever found any Sagalla caecilians on this property?. For the second question, eight  
206 images were carefully selected for clarity and unambiguity and presented to the  
207 respondent, including two images of *B. niedeni* and three species with similar  
208 morphology (two images of each). *B. niedeni* is commonly misidentified as either a  
209 worm or a snake, therefore we included images of both a common earthworm (phylum  
210 Annelida) and a regionally abundant, similarly coloured snake (genus *Amblyodipsas*).  
211 Lastly, pictures of a Southeast Asian caecilian (genus *Ichthyophis*) which have a striking  
212 yellow stripe along the length of their body and are therefore impossible to confuse with  
213 *B. niedeni* were included as a control (Fig. S1, supplementary materials). The purpose  
214 of this was to verify the landowner's ability to recognise the caecilian from multiple  
215 options, prior to collecting data on its predicted presence at the site.

216

217 *Statistical analysis*

218 While occupancy modelling was originally planned using the three replicate plots at  
219 each site as repeat observations, it was not possible due to a lack of any repeat  
220 observations in the dataset, a well-recognised problem with occupancy models running  
221 on sparse data (Welsh et al. 2013). We therefore analysed apparent occupancy  
222 (effectively the product of true occupancy and detection probabilities) without correcting  
223 for variation in detectability.

224 Generalised Linear Mixed Effects Models (GLMM) with binomial errors were run  
225 in the software R (R Core Team, 2015) using the presence/absence of *B. niedeni* as a  
226 response variable and a set of environmental data as explanatory variables (full set of  
227 variables collected in Table S1, supplementary materials) Explanatory variables were  
228 first grouped according to collinearity, and those considered most likely to have an  
229 effect on caecilian distribution, based on a review of the caecilian literature and  
230 consultation with experts, were retained as fixed effects: These were: land use type,  
231 surface soil temperature, soil compactness, and landowner prediction of caecilian  
232 presence.

233 Land use type was included in the model because it is hypothesised to play an  
234 important role in determining caecilian habitat use and therefore distribution, as  
235 evidenced by several recent studies reporting higher densities of caecilians from  
236 agricultural land than adjacent indigenous habitat (Hebrard et al. 1992; Oommen et al.  
237 2000; Gower & Wilkinson, 2005; Malonza et al. 2016; Jared et al. 2015).

238 Three environmental variables, soil moisture, soil pH, and ambient light, were  
239 disregarded prior to data analysis, due to suspected inaccuracy of the equipment used

240 in the field as the readings reported by the meter were the same when soil was visibly  
241 moist and visibly dry. Soil surface temperature and soil compactness were selected  
242 both to test their own effects on caecilian distribution and to serve as proxies for  
243 weather conditions and soil type, respectively. Several caecilian species have been  
244 shown to exhibit preferences for less compacted soil (Ducey et al. 1993) and soil  
245 compaction is considered a potential threat to *B. niedeni* (Malonza, 2016) but one that  
246 has not yet been quantified. Finally, the landowner prediction variable was included to  
247 test the hypothesis that local ecological knowledge may be a more efficient method to  
248 gather data on the presence of a particular amphibian species (Harpalini et al. 2015;  
249 Pan et al. 2016; Turvey et al. 2018; Kanagavel et al. 2020).

250 A random effect of site identity was used to account for spatial dependency  
251 between multiple plots dug at each sample site and thus avoid risk of pseudoreplication.  
252 All possible combinations of the four fixed effects were fitted (16 models in total), and  
253 Akaike weights were used to evaluate strengths of evidence for particular models and  
254 variable effects (Burnham & Anderson, 2002). The maximal importance scores of each  
255 variable were assessed by summing the Akaike weights of all models with that variable,  
256 with a score close to 1 denoting a strong effect while one <0.8 would indicate little to no  
257 effect. We limited our models for consideration to those within 6 AIC units of the top  
258 model (Richards, 2008). We also applied the 'nesting rule' within this model set, wherein  
259 models that are more complex versions of those that have a lower AIC are disregarded  
260 (Richards, 2008).

261 To test support for size-based clusters among captured caecilians, partitioning  
262 around medoids was used, with optimum number of clusters evaluated by average  
263 silhouette width (Hennig 2023).

264 Minimum caecilian densities, allowing for the possibility that not all individuals  
265 within plots would be found, were estimated by dividing numbers of caecilians found by  
266 the area of plot sampled, with standard errors and log normal confidence intervals  
267 derived from the empirical between-site variance in density (Borchers et al. 2002). Total  
268 population size was estimated by multiplying estimated density by total area of the site  
269 within which the survey was planned (1216 ha).

270

## 271 **Results**

272

### 273 *Sample characteristics*

274 Of the 228 plots dug at 76 systematically sampled sites, 112 (49.1%) were in  
275 agricultural areas, 71 (31.1%) in areas of high human disturbance, such as school  
276 yards, households, or plantations of eucalyptus or pine, and 45 (19.7%) in natural areas  
277 minimally affected by the human population, such as unmanaged, shrubby areas and  
278 the last remaining patch of the indigenous forest on Sagalla Hill.

279 In total, 31 caecilians were collected in 15 of the 228 plots, representing an  
280 encounter rate of 6.6% and a catch per unit effort of 0.15 caecilians per hour  
281 Disaggregating into land use types, plots dug in agricultural fields saw an encounter rate  
282 of 7.1% (8/112), while those dug in areas of high disturbance had 7.0% (5/71) and the  
283 natural areas were lowest with 4.4% (2/45). See Fig. 1 for a site map identifying plots

284 where caecilians were encountered at systematically selected sites. An additional 25  
285 caecilians were captured in ten of the 63 opportunistically surveyed plots (15.8%  
286 encounter rate). Three caecilians (5.6%) were severely injured during excavation and  
287 were euthanised.

288 The first plots dug at the pre-determined GPS marker for each sites contained  
289 fewer caecilians than the second and third plots that were dug in favourable caecilian  
290 microhabitat within 100 m of the GPS markers. Five out of the 31 caecilians were found  
291 at the systematically selected sites whereas the favourable caecilian microhabitat, held  
292 26/31 of the specimens encountered.

293 Overall, captured individuals averaged 2.6 g in weight (range 0.4 – 7.2 g) and  
294 200 mm in length (range 95 – 310 mm), but cluster analysis strongly supported the  
295 existence of two size groups (Fig. 2). Smaller individuals (presumed juveniles, n = 22)  
296 averaged 0.8 g (0.4 – 1.8 g) and 128 mm (95–180 mm) while larger individuals  
297 (presumed adults, n=29) averaged 3.9 g (2.8–6.4 g) and 254 mm (220 – 310 mm).

298

#### 299 *Landowner prediction survey*

300 Of the 228 plots dug, 61.0% (139/228) were on private land, requiring that a landowner  
301 be approached for permission, while the remaining sites were located on public land.

302 Of the 139 landowners approached, 87.8% (122/139) correctly identified *B. niedeni* from  
303 the four images presented to them. Of these 122 landowners, 79.5% (97/122) confirmed  
304 that they had found the caecilians on their property before. This suggests that  
305 landowners potentially hold good information on caecilian presence. Furthermore, the  
306 encounter rate at these 97 plots where presence of caecilians were reported was 8.3%

307 (8/97), compared with 0% (0/25) for plots on land where the owner did not report  
308 caecilians.

309

### 310 *Mixed Effects Modelling*

311 Of the remaining four predictors of the probability of encountering caecilians at a site,  
312 none showed any clear evidence of an effect. All models within the top set were nested  
313 versions of the top model (the null model), suggesting that they should be disregarded  
314 from consideration, and maximal important scores were low for all variables (0.46 for  
315 soil surface temperate in the highest case; Table 1).

316

### 317 *Density*

318 Caecilian density in plots selectively located in habitat expected to be favourable for  
319 caecilians at systematically selected sites was estimated at 721 ha<sup>-1</sup> (SE 261, log  
320 normal 95% confidence interval 282 – 1287) or 0.07 m<sup>2</sup>. While a return of only five  
321 individuals at a single randomly selected plot prevents precise estimation, we can  
322 tentatively calculate a lower site wide average density of 347 ha<sup>-1</sup> (SE 347, log normal  
323 95% confidence interval 68 – 1775) or 0.03 m<sup>2</sup>. Extrapolating the average density per  
324 ha to the entire study area suggests a total population of 422,222 (CI 82,576 –  
325 2,158,867).

326

327

### 328 **Discussion**

329 Taken together, we suggest that our results indicate a degree of cautious optimism  
330 regarding the status of *B. niedeni*. Although we found the species in only a small  
331 proportion of sample plots (6.6%), we believe that this low encounter rate largely reflects  
332 the low efficiency of our survey method. Caecilians are inhabitants of moist forest, and  
333 their localised distribution is usually strongly correlated with soil moisture (Gundappa et  
334 al. 1981; Gower and Wilkinson 2005; Kupfer et al. 2005; Jared et al., 2015; Wake 1994;  
335 Malonza, 2016). The absence of soil moisture and light intensity data is therefore a  
336 significant shortfall of this study. However, for the variables we did explore, we found no  
337 strong habitat associations, suggesting that the species is adaptable and able to exploit  
338 a range of habitats, including heavily disturbed land uses. This suggests that much of  
339 the species' range remains habitable, despite widespread and intense disturbance.  
340 Consistent with this, a large majority (80%) of farmers reported the presence of the  
341 species on their land. Furthermore, even without correcting for imperfect detectability,  
342 abundance in the targeted plots was substantial, with an estimated density of around  
343 350 caecilians per hectare overall, and twice that in favourable habitat. Furthermore,  
344 these density estimates could be an underestimate if caecilians were able to react to  
345 digging by escaping from the plot before being detected, or if caecilians typically burrow  
346 below 30 cm depth in the soil. While our overall density estimate from randomly located  
347 plots is tentative due to the small number of caecilians discovered, taken together, our  
348 results suggest that the total *B. niedeni* population could well number in the hundreds of  
349 thousands. Density estimates for *B. niedeni* in favourable habitat are similar to  
350 density estimates reported for two congeneric species (*B. boulengeri* and *B. taitana*)  
351 from forest habitat at a similar time of year (Measey, 2004; Measey & Barot, 2006).



352 Finally, caecilians encountered were clearly grouped in two distinct size and weight  
353 classes which we interpret as juveniles and adults, suggesting ongoing breeding and  
354 potential recruitment.

355 No effects of land use type, soil temperature or compaction, and landowner  
356 knowledge had a detectable association with the presence of caecilians. This lack of  
357 any effect of habitat types on caecilian presence may be due to the species' adaptability  
358 to anthropogenically disturbed habitats (Gower & Wilkinson, 2005; ). Combined with the  
359 relatively small area of indigenous vegetation remaining on Sagalla Hill, these caecilians  
360 may have little choice but to occupy modified landscapes. Moreover, this is consistent  
361 with the findings of a number of caecilian studies (Hebrard et al. 1992; Oommen et al.  
362 2000; Jared et al. 2015), which hypothesised that the benefits of irrigation in agricultural  
363 fields may outweigh the drawbacks of living in a disturbed habitat. Indeed, many  
364 agricultural fields in Sagalla are irrigated, particularly those near the Sagalla river. While  
365 the encounter rates found in this study were lower than in previous surveys of other  
366 caecilian species at a similar time of year (Oommen et al. 2000; Measey et al. 2003;  
367 Malonza & Measey, 2005), this may not be representative of a decline in abundance as  
368 the site selection process in our study used a different sampling design (evenly spaced  
369 and random rather than grouped in areas with high probability of caecilian occurrence).

370 The reproductive mode of *Boulengerula niedeni* is not known for certain. The  
371 closely related species *B. taitanus* is oviparous and has altricial young that are nursed  
372 via the hypertrophic skin secretions of the female (Malonza & Measey, 2005; Kupfer et  
373 al. 2006). The altricial young of *B. taitanus* have a total length of approximately 28 mm  
374 when they hatch (Kupfer et al. 2006), are unpigmented and undergo an ontogenetic

375 shift in pigmentation becoming increasingly pigmented, with pigmentation developing  
376 from a darker middorsal band which gradually broadens over time (Nussbaum & Hinkel,  
377 1994). The young become independent of their mothers when they reach approximately  
378 86 mm in length (Kupfer et al. 2006). Females of this species have an annual  
379 reproductive cycle (Raquet et al. 2015) and they are known to nest in January after the  
380 short rainy season (Kupfer et al. 2006). It is likely that this reproductive mode is also  
381 exhibited by *B. niedeni* and that our surveys therefore took place after the breeding and  
382 nesting season. The few juvenile *B. niedeni* that are known were unpigmented on their  
383 ventral and lateral surfaces (Müller et al. 2005), indicating that a similar ontogenetic shift  
384 in colouration also occurs in this species. The smallest individual *B. niedeni* we  
385 encountered had a total length of 95 mm and all were well pigmented. No nests were  
386 excavated which could reflect seasonality of breeding but nests might have been  
387 missed. The bimodality in the caecilian morphometric data (Fig. 2) reveals two clear  
388 size categories of specimens which might indicate ongoing breeding as well as the  
389 presence of an annual breeding cycle like other congeneric species.

390  
391 Our sampling strategy encountered a number of operational difficulties on the ground,  
392 namely due to the inherently destructive nature of the sampling protocol. Indeed,  
393 combined with the local dependence on subsistence agriculture, farmers would  
394 understandably not allow any part of their field to be dug up while their crops were  
395 sown. For this reason, many of our plots were forced away from their systematically  
396 placed GPS marker, introducing bias to the random sampling portion of the survey. This  
397 also may cause slightly sub-optimal habitat to be sampled in our first plots, as fields are

398 often fringed by hedgerows, streams, or roads. One solution to this issue could be to  
399 synchronise future caecilian surveys with the annual harvest that occurs in February in  
400 Sagalla, so that the soil is only disturbed once. Additionally, any additional caecilian  
401 mortality caused by the digging process would be minimised by sampling during a  
402 regular digging event that would occur either way, while also allowing for a greater  
403 volume of soil to be sampled. However this might risk disturbing nests if caecilians  
404 breed at this time of year. Such a strategy should not be undertaken in habitat types  
405 that would otherwise be undisturbed until more information on the time of breeding and  
406 parental care is known. This information might be gathered by the further questioning of  
407 local land users.

408 Another important limitation to our study was the failure to account for imperfect  
409 detection of caecilians while sampling the survey sites, for a number of reasons. First,  
410 due to the high amount of effort needed to manually excavate the soil, only a relatively  
411 small volume of soil was sampled in comparison to the total volume available to the  
412 species. Second, caecilians would have likely been disturbed at the onset of digging  
413 and could have moved out of the plot before they were excavated. It should however be  
414 mentioned that an escape response was not clearly evident in our field experience, as  
415 in many cases the caecilians captured from a plot were discovered after digging had  
416 been ongoing for a few minutes. Third, it is possible, but unlikely, that caecilians may  
417 have been excavated but not spotted by either of the diggers, thus allowing the  
418 individuals to escape back into the soil.

419 The primary limitation inhibiting statistical analysis of the data was the low  
420 encounter rate of caecilians (15/228 plots, 6.9%). There are several ways in which

421 future caecilian surveys could increase their encounter rate. Some avenues for future  
422 exploration include the potential use of eDNA (Thomsen & Willerslev, 2015) in the  
423 detection of caecilian presence within the soil using easily extracted soil cores. If viable,  
424 this would allow sampling without crop disruption while also shedding light on depths of  
425 caecilians activity. Secondly, a caecilian survey with mechanical digging would  
426 decrease the effort involved while increasing the speed at which the soil is removed,  
427 thus minimising the likelihood of missing individuals due to an escape response.  
428 However mechanical excavators are expensive and cumbersome and, in many cases,  
429 including Sagalla Hill, would be unable to reach sites targeted during a caecilian survey,  
430 thus only under very specific circumstances could their superior digging power be  
431 effectively used.

432         The landowner prediction survey showed that most landowners were able to  
433 correctly identify the target species and that of these, 79.5% of respondents had  
434 encountered *B. niedeni* on their property before. The encounter rate of *B. niedeni* at  
435 plots where presence of caecilians was reported was relatively high and no caecilians  
436 were detected in plots where land owners did not report the presence of the species.  
437 This is consistent with landowners providing reliable reports of caecilian presence,  
438 although the small sample of absences here precludes strong conclusions on this. A  
439 limitation with our survey strategy was that we did not ask when *B. niedeni* was last  
440 seen. The climate and land use may have changed over time and once suitable habitat  
441 may have become unsuitable. Whilst our work shows that information from local  
442 respondents may be of use in providing information on this particular species, future  
443 studies should include estimates of last sighting date. Surveys on fossorial vertebrates

444 have a unique set of challenges, setting them quite apart from the average ecological  
445 survey of cryptic species (e.g., Gower & Wilkinson, 2005; Measey, 2006). Our  
446 ecological survey of *B. niedeni* highlighted these challenges but nonetheless produced  
447 some interesting findings to advance our knowledge of the species. We provide the first  
448 population estimate for the species which provides an important baseline for the future  
449 study of population trends overtime. Furthermore, this work supports the growing  
450 evidence for apparent tolerance for agricultural and human-disturbed habitat as well as  
451 evidence of ongoing breeding. While their apparent survival in human-disturbed  
452 landscapes may warrant cautious optimism, the species remains a narrow-range  
453 endemic, necessarily restricted to a very small area. *B. niedeni* was first assessed as  
454 Critically Endangered in 2006 on the basis of its extremely limited extent of occupancy,  
455 although it was later down listed to Endangered (EN) in 2012 (IUCN, 2020). The current  
456 assessment is very close to becoming out-of-date. Our study indicates that *B. niedeni*  
457 probably still qualifies for being assessed as En in accordance with the IUCN Red List  
458 of Threatened Species categories and criteria B1ab(iii) (see IUCN, 2012).

459 More generally, there remains an urgent need to enhance our understanding and  
460 protection of soil ecosystems worldwide. It is hoped that our study can inform similar  
461 work for caecilians and other fossorial vertebrates.

462

#### 463 **Acknowledgements**

464 The authors are grateful to the National Museums of Kenya and the Taita Taveta  
465 Wildlife Forum for their invaluable assistance in the field, as well as to the Zoological  
466 Society of London, the EDGE of Existence Programme, the Institute of Zoology, and

467 Imperial College London for essential support and guidance of this research. Finally, the  
468 people of Sagalla are warmly thanked for their hospitality and support during data  
469 collection.

#### 470 **References**

- 471 Bhatta, G. (1997). Caecilian diversity of the Western Ghats: in search of the rare  
472 animals. *Current Science*, 73, 183–187.
- 473 British Herpetological Society (2017). British Herpetological Society: Ethical policy and  
474 guidelines. *Herpetological Bulletin*, 141, 46–48.
- 475 Burnham, K. & Anderson, D. (2002). Information and likelihood theory: a basis for model  
476 selection and inference. *Model Selection and Multimodel Inference: A Practical*  
477 *Information-Theoretic Approach*, 49–97.
- 478 Copley, J. (2000). Ecology goes underground. *Nature*, 406 (6795), 452–454.  
479 <https://doi.org/10.1038/35020131>
- 480 de Oliveira Ferronato, B. (2019). An assessment of funding and publication rates in  
481 Herpetology. *Herpetological Journal*, 29 (4), 264–273.  
482 <https://doi.org/10.33256/hj29.4.264273>
- 483 Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G. & Lavelle, P. (2006). The values of  
484 soil animals for conservation biology. *European Journal of Soil Biology*, 42 (1),  
485 S23–S38. <https://doi.org/10.1016/j.ejsobi.2006.07.001>
- 486 Ducey, P.K., Formanowicz Jr, D.R., Boyet, L., Mailloux, J. & Nussbaum, R.A. (1993).  
487 Experimental examination of burrowing behavior in caecilians (Amphibia:

488 Gymnophiona): effects of soil compaction on burrowing ability of four  
489 species. *Herpetologica*, 49 (4), 450–457.

490 Gaborieau, O. & Measey, G.J. (2004). Termitivore or detritivore? A quantitative  
491 investigation into the diet of the East African caecilian *Boulengerula taitanus*  
492 (Amphibia: Gymnophiona: Caeciliidae). *Animal Biology*, 54 (1), 45–56.

493 Gower, D.J. & Wilkinson, M. (2005). Conservation biology of caecilian amphibians.  
494 *Conservation Biology*, 19 (1), 45–55. [https://doi.org/10.1111/j.1523-  
495 1739.2005.00589.x](https://doi.org/10.1111/j.1523-1739.2005.00589.x)

496 Gumbs, R., Gray, C.L., Wearn, O.R. & Owen, N.R. (2018). Tetrapods on the EDGE:  
497 Overcoming data limitations to identify phylogenetic conservation priorities. *PLoS*  
498 *One*, 13 (4), e0194680. <https://doi.org/10.1371/journal.pone.0194680>

499 Gundappa, K.R., Balakrishna, T. A. & Shakuntala, K. (1981). Ecology of *Ichthyophis*  
500 *glutinosus* (Linn.) (Apoda, Amphibia). *Current Science*, 50, 480 – 483.

501 Harpalani, M., Parvathy, S., Kanagavel, A., Eluvathingal, L.M. & Tapley, B. (2015). Note  
502 on range extension, local knowledge and conservation status of the Critically  
503 Endangered Anamalai gliding frog *Rhacophorus pseudomalabaricus* in the  
504 Cardamom Hills of Western Ghats, India. *The Herpetological Bulletin*, 133, 1–6.

505 Hebrard, J.J., Maloiy, G.M. & Alliangana, D.M. (1992). Notes on the habitat and diet of  
506 *Afrocaecilia taitana* (Amphibia: Gymnophiona). *Journal of Herpetology*, 26 (4),  
507 513–515.

508 Hennig, C. (2023). R package fpc: Flexible Procedures for Clustering, version 2.2-10,  
509 <https://CRAN.R-project.org/package=fpc>.

510 Isaac, N.J., Redding, D.W., Meredith, H.M. & Safi, K. (2012). Phylogenetically-informed  
511 priorities for amphibian conservation. *PLoS One*, 7 (8), e43912.  
512 <https://doi.org/10.1371/journal.pone.0043912>

513 IUCN SSC Amphibian Specialist Group (2013). *Boulengerula niedeni*. The IUCN Red  
514 List of Threatened Species 2013: e.T61920A13322136. Downloaded on 16  
515 March 2021. <https://dx.doi.org/10.2305/IUCN.UK.2013->  
516 [2.RLTS.T61920A13322136.en](https://dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T61920A13322136.en).

517 IUCN (2012). IUCN Red List Categories and Criteria: version 3.1.. 2nd ed. Gland,  
518 Switzerland and Cambridge, UK: IUCN; p. iv + 32.

519 Jared, C., Antoniazzi, M.M., Wilkinson, M. & Delabie, J.H. (2015). Conservation of the  
520 caecilian *Siphonops annulatus* (Amphibia, Gymnophiona) in Brazilian cacao  
521 plantations: a successful relationship between a fossorial animal and an  
522 agrosystem. *Agrotrópica*, 27(3), 233–238.  
523 DOI: 10.21757/0103-3816.2015v27n3p233-238

524 Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P. & Lepage, M. (2006). Soil invertebrates  
525 as ecosystem engineers: intended and accidental effects on soil and feedback  
526 loops. *Applied Soil Ecology*, 32 (2), 153–164.  
527 <https://doi.org/10.1016/j.apsoil.2005.07.004>

528 Jones, D. T., S. P. Loader, & Gower, D.J. (2006). Trophic ecology of East African  
529 caecilians (Amphibia : Gymnophiona), and their impact on forest soil  
530 invertebrates. *Journal of Zoology*, 269, 117–126.  
531 <https://doi.org/10.1111/j.1469-7998.2006.00045.x>



532 Kanagavel, A., Parvathy, S., Tapley, B., Nirmal, N., Selvaraj, G., Raghavan, R., Murray,  
533 C., Owen, N. & Turvey, S.T. (2020). Are local and traditional ecological  
534 knowledge suitable tools for informing the conservation of threatened amphibians  
535 in a biodiversity hotspot? *Herpetological Bulletin*, 153, 3–13.

536 Kouete, M. T. & Blackburn, D.C. (2020). Dietary partitioning in two co-occurring  
537 caecilian species (*Geotrypetes seraphini* and *Herpele squalostoma*) in Central  
538 Africa. *Integrative Organismal Biology*, 2, obz035.  
539 <https://doi.org/10.1093/iob/obz035>

540 Kupfer, A., Nabhitabhata, J. & W. Himstedt (2005). From water into soil: trophic ecology  
541 of a caecilian amphibian (genus *Ichthyophis*). *Acta Oecologica*, 28, 95–105.  
542 <https://doi.org/10.1016/j.actao.2005.03.002>

543 Kupfer, A., Müller, H., Antoniazzi, M.M., Jared, C., Greven, H., Nussbaum, R.A. &  
544 Wilkinson, M. (2006). Parental investment by skin feeding in a caecilian  
545 amphibian. *Nature*, 440 (7086), 926–929.  
546 doi: 10.1038/nature04403.

547 Largen, M., Morris, P. & Yalden, D. (1972). Observations on the caecilian *Geotrypetes*  
548 *grandisonae* Taylor (Amphibia: Gymnophiona) from Ethiopia. *Pubblicazioni del*  
549 *centro di studio per la faunistica ed ecologia tropicali del CNR LX. Monitore*  
550 *Zoologico Italiano*, 4 (1), 185–205.

551 Lavelle, P., Bignell, D., Lepage, M., Wolters, W., Roger, P., Ineson, P., Heal, O. &  
552 Dhillon, S. (1997). Soil function in a changing world: the role of invertebrate  
553 ecosystem engineers. *European Journal of Soil Biology*, 33 (4), 159–193.

554 Luedtke, J.A., Chanson, J., Neam, K., Hobin, L., Maciel, A.O., Catenazzi, A., Borzée,  
555 A., Hamidy, A., Aowphol, A., Jean, A., Sosa-Bartuano, Á., Fong G., de Silva, A.,  
556 Fouquet, A., Angulo, A., Kidov, A.A., Muñoz Saravia, A., Diesmos, A.C.,  
557 Tominaga, A., Shrestha, B., Gratwicke, B. Tjaturadi, B., Martínez Rivera, C.C.,  
558 Vásquez Almazán, C.R., Señaris, C., Chandramouli, S.R., Strüssmann, C.,  
559 Cortez Fernández, C. F., Azat, C., Hoskin, C.J., Hilton-Taylor, C., Whyte, D.L.,  
560 Gower, D.J., Olson, D.H., Cisneros-Heredia, D.F., Santana, D.J., Nagombi, E.,  
561 Najafi-Majd, E., Quah, E.S.H., Bolaños, F., Xie, F., Brusquetti, F., Álvarez, F.S.,  
562 Andreone, F., Glaw, F., Castañeda, F.E, Kraus, F., Parra-Olea, G., Chaves, G.,  
563 Medina-Rangel, G.F., González-Durán, G., Ortega-Andrade, H.M., Machado,  
564 I.F., Das, I., Dias, I.R., Urbina-Cardona, J.N., Crnobrajica-Isailović, J., Yang, J-H.,  
565 Jianping, J., Wangyal, J.T., Rowley, J.J.L., Measey, J., Vasudevan, K., Chan,  
566 K.O., Gururaja, K.V.Ovaska, K., Warr, L.C., Canseco-Márquez, L., Toledo, L.F.,  
567 Díaz, L.M., Khan, M.M.H., Meegaskumbura, M., Acevedo, M.E., Napoli, M.F.,  
568 Ponce, M.A., Vaira, M., Lampo, M., Yáñez-Muñoz, M.H., Scherz, M.D., Rödel, M.,  
569 Matsui, M., Fildor, M., Kusriani, M.D., Ahmed, M.F., Rais, M., Kouamé, N.G.,  
570 García, N., Gonwouo, N.L., Burrowes, P.A., Imbun, P.Y., Wagner, P., Kok,  
571 Philippe J. R., Joglar, R.L., Auguste, R.J., Brandão, R.A., Ibáñez, R., von May,  
572 R., Hedges, S.B., Biju, S.D., Ganesh, S.R., Wren, S., Das, S., Flechas, S.V.,  
573 Ashpole, S.L., Robleto-Hernández, S.J., Loader, S.P., Incháustegui, S.J., Garg,  
574 S., Phimmachak, S., Richards, S.J., Slimani, T., Osborne-Naikatini, T., Abreu-  
575 Jardim, T.P.F., Condez, T.H., De Carvalho, T.R., Cutajar, T. P., Pierson, T.W.,  
576 Nguyen, T.Q., Kaya, U., Yuan, Z., Long, B., Langhammer, P., Stuart, S.N. 2023.

577 Ongoing declines for the world's amphibians in the face of emerging  
578 threats. *Nature*, 622, 308–314  
579 <https://doi.org/10.1038/s41586-023-06578-4>

580 Loader, S.P., Gower, D.J. & Wilkinson, M. (2003). Caecilians: mysterious amphibians of  
581 the Eastern Arc Mountains. *Arc Journal*, 153–4.

582 Malonza, P.K. (2016). Conservation education and habitat restoration for the  
583 endangered Sagalla caecilian (*Boulengerula niedeni*) in Sagalla Hill,  
584 Kenya. *Zoological Research*, 37 (3), 159–166.  
585 DOI: [10.13918/j.issn.2095-8137.2016.3.159](https://doi.org/10.13918/j.issn.2095-8137.2016.3.159)

586 Malonza, P.K., Lötters, S. & Measey, G.J. (2010). The montane forest associated  
587 amphibian species of the Taita Hills, Kenya. *Journal of East African Natural  
588 History*, 99 (1), 47–63.

589 Malonza, P.K. & Measey, G.J. (2005). Life history of an African caecilian: *Boulengerula  
590 taitanus* Loveridge 1935 (Amphibia Gymnophiona Caeciliidae). *Tropical  
591 Zoology*, 18 (1), 49–66.  
592 <https://doi.org/10.1080/03946975.2005.10531214>

593 Measey, G.J. (2004). Are caecilians rare? An east African perspective. *Journal of East  
594 African Natural History*, 93 (1), 1–21.

595 Measey, G. (2006). Surveying biodiversity of soil herpetofauna: towards a standard  
596 quantitative methodology. *European Journal of Soil Biology*, 42 (Supplement 1)  
597 S103–S110.

598 Measey, G.J., Armstrong, A.J. & Hanekom, C. (2009). Subterranean herpetofauna show  
599 a decline after 34 years in Ndumu Game Reserve, South Africa. *Oryx*, 43 (02),  
600 284–287. doi:10.1017/S0030605307002311

601 Measey, G.J. & Barot, S. (2006). Evidence of seasonal migration in a tropical  
602 subterranean vertebrate. *Journal of Zoology*, 269 (1), 29–37.  
603 <https://doi.org/10.1111/j.1469-7998.2005.00039.x>

604 Measey, G., Gower, D., Oommen, O. & Wilkinson, M. (2003). Quantitative surveying of  
605 endogeic limbless vertebrates—a case study of *Gegeneophis ramaswamii*  
606 (Amphibia: Gymnophiona: Caeciliidae) in southern India. *Applied Soil Ecology*,  
607 23 (1), 43–53. [https://doi.org/10.1016/S0929-1393\(02\)00175-0](https://doi.org/10.1016/S0929-1393(02)00175-0)

608 Measey, J.G., Mejissa, J. & Müller, H. (2006). Notes on the distribution and abundance  
609 of the caecilian *Boulengerula uluguruensis* (Amphibia: Gymnophiona:  
610 Caeciliidae) in the Uluguru Mountains, Tanzania. *African Journal of Ecology*, 44  
611 (1), 6–13.  
612 <https://doi.org/10.1111/j.1365-2028.2006.00569.x>

613 Measey, J.G., Muchai, V. & Spawls, S. (2012). Rediscovery of *Boulengerula denhardti*  
614 Nieden 1912 (Amphibia: Gymnophiona: Caeciliidae) in Meru County,  
615 Kenya. *African Zoology*, 47(1), 187–191.

616 Müller, H., Measey, G.J., Loader, S.P. & Malonza, P.K. (2005). A new species of  
617 *Boulengerula* Tornier (Amphibia: Gymnophiona: Caeciliidae) from an isolated  
618 mountain block of the Taita Hills, Kenya. *Zootaxa*, 1004 (1), 37–50.  
619 <https://doi.org/10.11646/zootaxa.1004.1.4>

620 Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000).  
621 Biodiversity hotspots for conservation priorities. *Nature*, 403 (6772), 853–858.  
622 <https://doi.org/10.1038/35002501>

623 Nature Kenya, National Museums of Kenya, Kenya Wildlife Service & Kenya Forest  
624 Service. 2015. Single Species Action plan for Conservation of Sagalla Caecilian  
625 (*Boulengerula niedeni*): 2015-2020. Nairobi: Kenya Wildlife Service. 11pp.

626 Nussbaum, R.A. & Hinkel, H. (1994). Revision of East African caecilians of the genera  
627 *Afrocaecilia* Taylor and *Boulengerula* Tornier (Amphibia: Gymnophiona:  
628 Caeciliidae). *Copeia*, 1994, 750–760.  
629 <https://doi.org/10.2307/1447192>

630 Oommen, O.V., Measey, G.J., Gower, D.J. & Wilkinson, M. (2000). Distribution and  
631 abundance of the caecilian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona)  
632 in southern Kerala. *Current Science-Bangalore-*, 79 (9), 1386–1389.

633 Pan, Y., Wei, G., Cunningham, A.A., Li, S., Chen, S., Milner-Gulland, E.J. & Turvey,  
634 S.T. (2016). Using local ecological knowledge to assess the status of the  
635 Critically Endangered Chinese giant salamander *Andrias davidianus* in Guizhou  
636 Province, China. *Oryx*, 50 (2), 257–64. doi:10.1017/S0030605314000830

637 Pooley, A., Pooley, E., Hadley, W. & Gans, C. (1973). Ecological aspects of the  
638 distribution of subsoil herpetofauna in Ndumu Game Reserve. *Annals of the*  
639 *Carnegie Museum*, 44, 103–115.

640 Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M P., Foster,  
641 P.N., La Marca, E., Masters, K.L., Merino-Viteri, A. & Puschendorf, R. (2006).

642 Widespread amphibian extinctions from epidemic disease driven by global  
643 warming. *Nature*, 439 (7073), 161–167. <https://doi.org/10.1038/nature04246>

644 R Core Team (2015). R: A language and environment for statistical computing. R  
645 Foundation for Statistical Computing, Vienna, Austria. URL Downloaded on 16  
646 March 2021. <https://www.R-project.org/>.

647 Raquet, M.A., Exbrayat, J.M. & Measey, G.J. (2015). Annual variation of ovarian  
648 structures of *Boulengerula taitana* (Loveridge 1935), a Kenyan caecilian. *African*  
649 *Journal of Herpetology*, 64 (2), 116–134.  
650 <https://doi.org/10.1080/21564574.2015.1103787>

651 Richards, S.A. (2008). Dealing with overdispersed count data in applied  
652 ecology. *Journal of Applied Ecology*, 45 (1), 218–227.

653 Scheele, B.C., Pasmans, P., Skerratt, L.F., Berger, L., Martel, A., Beukema, W.,  
654 Acevedo, A.A., Burrowes, P.A., Carvalho, T., Catenazzi, A. & De la Riva, I.  
655 (2019). Amphibian fungal panzootic causes catastrophic and ongoing loss of  
656 biodiversity. *Science*, 363, 1459–463.  
657 <https://www.science.org/doi/10.1126/science.aav0379>

658 Thomsen, P.F. & Willerslev, E. (2015). Environmental DNA—an emerging tool in  
659 conservation for monitoring past and present biodiversity. *Biological*  
660 *Conservation*, 183, 4–18. <https://doi.org/10.1016/j.biocon.2014.11.019>

661 Turvey, S.T., Chen, S., Tapley, B., Wei, G., Xie, F., Yan, F., Yang, J., Liang, Z., Tian,  
662 H., Wu, M., Okada, S., Wang, J., Lü, J., Zhou, F., Papworth, S.K., Redbond, J.,  
663 Brown, T., Che, J. & Cunningham, A.A. (2018). Imminent extinction in the wild of

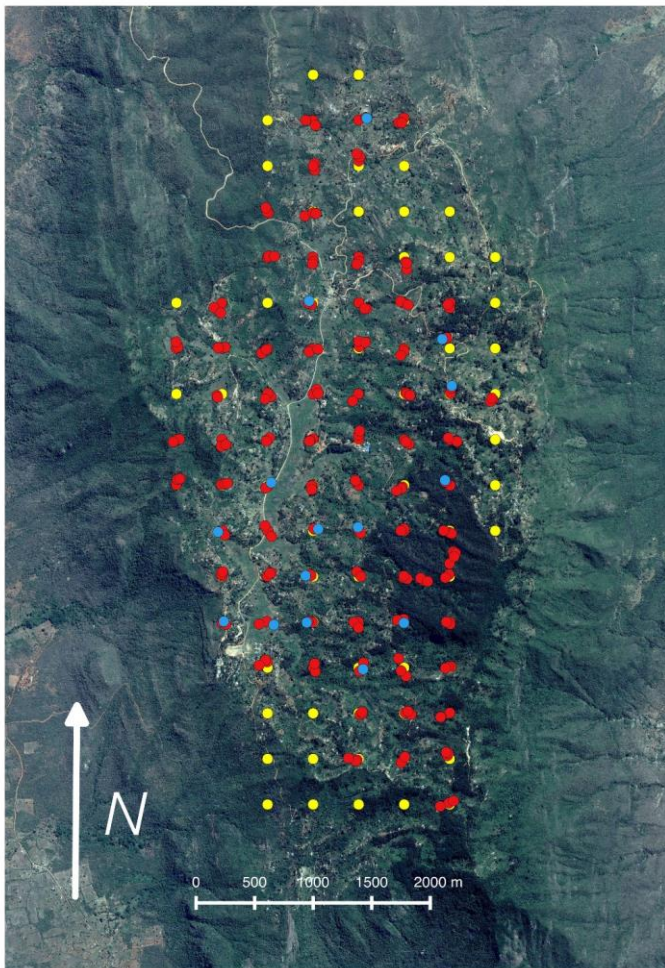
664 the world's largest amphibian. *Current Biology*, 28, R592–R594.  
665 <https://doi.org/10.1016/j.cub.2018.04.005>

666 Wake, D.B. & Vredenburg, V.T. (2008). Colloquium paper: are we in the midst of the  
667 sixth mass extinction? A view from the world of amphibians. *Proceedings of the*  
668 *National Academy of Sciences of the United States of America*, 105 (Supplement  
669 1), 111466–11473. <https://doi.org/10.1073/pnas.0801921105>

670 Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013). Fitting and interpreting  
671 occupancy models. *PLoS One*, 8 (1), p.e52015.  
672 <https://doi.org/10.1371/journal.pone.0052015>

673 Wojnowski, D. & Malonza, P.K. (2009). Kilima-Mrota is not a worm: the effect of  
674 conservation education and a local naming contest on the perspectives held by  
675 the peoples of Sagalla Hill, Kenya toward the Sagalla Caecilian *Boulengerula*  
676 *niederi*. *Journal of East African Natural History*, 98 (2), 241–248.  
677 <https://doi.org/10.2982/028.098.0205>  
678

679 **Figure 1.** Sagalla caecilian survey sites, including unsampled locations in yellow, and  
680 surveyed sites in blue (caecilian present) and red (no caecilians found) on Sagalla Hill,  
681 Kenya. Note supplementary sampling in the indigenous forest habitat (darker green).



682

**Commented [Rev1]:** Figure 1 change "lower mid-right side" to a geographic area. Is the entire forested area one big indigenous patch (as suggested) or is some plantation forest to be restored?

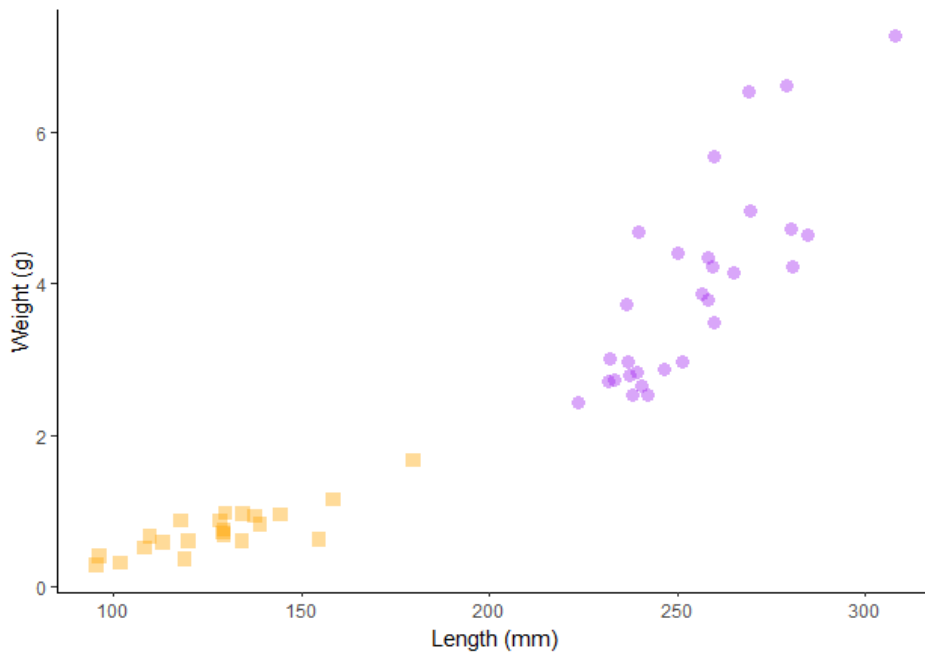
**Commented [Rev2R1]:** David / Basil - please could you advise?

**Commented [DM3R1]:** The forested area is divided between indigenous forest and plantations, but the oversampling was done only in the indigenous forest. Suggested change made in the text.



683 **Figure 2.** Length and weight distribution of specimens of *Sagalla caecilian*  
684 (*Boulengerula niedeni*) sampled in this study. Contrasting symbols and colours  
685 represent membership of the two groups identified by cluster analysis, likely  
686 representing age classes.

687  
688



689  
690  
691