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Spatial ecology of the Endangered and endemic Sagalla caecilian *Boulengerula niedeni* in the Eastern Arc Mountains of Kenya

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Caecilians (Order Gymnophiona) are generalist predators of soil invertebrates, and may therefore play an important role in tropical soil ecosystems. However, their fossorial lifestyle and the associated difficulties in surveying them have caused a deficit in data for the majority of species. We applied a systematic approach and an intensive sampling strategy to an Endangered and evolutionarily distinct caecilian from the Eastern Arc Mountains, the Sagalla caecilian *Boulengerula niedeni*. We investigated the association between habitat type and caecilian occupancy across its entire range, the Sagalla Hill, Kenya, and explored the relationship between several variables (land use type, surface soil temperature, soil compactness and landowner prediction of caecilian presence) and its presence in different habitats. We found no significant effects of any of the investigated variables in predicting caecilian presence across the Sagalla landscape. Instead, our findings suggest that the species survives at least as well in agricultural landscapes as it does in areas with indigenous vegetation, with an estimated density of around 900 caecilians per hectare. A bimodal distribution of sizes and weights of captured specimens suggests ongoing successful breeding and recruitment. This suggests that there is a case for cautious optimism with regard to the status of *B. niedeni*. Our work could act as a useful pilot for further, improved caecilian surveys in the Eastern Arc Mountains and beyond, to improve our understanding and conservation of these overlooked fossorial amphibians.

Keywords: amphibian, Gymnophiona, Herpelidae, soil ecology, amphibian conservation, Taita Hills

INTRODUCTION

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

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

Caecilians could also prove to be useful indicator species for soil ecosystems (Measey, 2006), particularly with the unpredictable effects that anthropogenic climate change is likely to have on soil ecosystems worldwide (Copley, 2000; Decaëns et al., 2006). With reports of several caecilian species being commonly encountered in low-intensity agricultural landscapes (Hebrard et al., 1992; Measey, 2004; Jared et al., 2015; Malonza, 2016), these species could be indicators of soil degradation or pesticide toxicity, though this requires more investigation (Oommen et al., 2000; Gower & Wilkinson, 2005).

A contributing factor to the paucity of caecilian research is the challenge of surveying them. Soil is an opaque, dense and heterogeneous medium that requires considerable energy and destructive force to sample comprehensively (Decaëns et al,. 2006; Measey, 2006). A basic component of caecilian surveys is manually

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excavating the soil, a labour-intensive process with a relatively low return in terms of the number of caecilians sighted per unit of effort expended, partly due to the often patchy yet poorly understood distribution of many caecilian species (Largen et al., 1972; Measey et al., 2003; Gower & Wilkinson, 2005). This challenge has inhibited the development of effective tools for measuring ecological parameters for most caecilian species, though efforts by Measey (2006) to develop a standardised methodology have been a step in the right direction. This challenge has resulted in over half (97/193) of caecilian species being assessed as Data Deficient by the IUCN (IUCN, 2023), with few quantitative historical datasets against which to compare current populations (Measey et al., 2009). For this reason, statements on declines in caecilian species are often founded on recent surveys having returned no individuals from sites of known historical presence (Gower & Wilkinson, 2005 and references therein), or inferences made from broader soil herpetofaunal declines (Pooley et al., 1973; Measey et al., 2009).

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

The objective of this study was to quantitatively assess the distribution and occupancy of *B. niedeni* across its distributional range, to better inform future conservation work aimed at protecting the biodiversity of Sagalla Hill. We sought to test if land use type was correlated with species' occurrence across this heavily altered landscape. An ancillary objective was to collect data on environmental and soil variables, to explore the species' preferred habitat conditions. To the best of our knowledge it is one of the most intensive sampling efforts of an African caecilian amphibian, and the first to sample at randomly selected sites across the entire range of a caecilian species.

MATERIALS & METHODS

Ethics and Biosecurity statement

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

Data collection

Fieldwork was carried out on Sagalla Hill in south-eastern Kenya (3.499° S, 38.580° E, 580–1450 metres above sea level) in May and June of 2016, in the transition season between the long rains (March−May) and the cooler, dry winter (June−September). Caecilians were sought at pre-determined sites on a systematic grid covering the whole of Sagalla Hill, with the intent to produce data for occupancy modelling. Given that the semi-arid lowland habitat surrounding Sagalla represents a barrier to amphibian dispersal and that the nearby Taita Hills have been well sampled and only ever produced the closely related yet distinct Taita caecilian *Boulengerula taitanus* (Malonza & Measey, 2005), we assumed that the entire range of *B. niedeni* was covered by this study. A three-person team visited 76 sites over 36 days, between the times of 07:00 h and 11:00 h to avoid the heat of mid-day. A total of 204.8 person hours were spent digging for caecilians. We estimated the total number of sites that could feasibly be visited within the planned research period and created a grid with this number of sites spaced evenly across the entire study area, resulting in a constant spacing of 400 m between sites (Fig. 1). This even spacing of sites ensured that all land use types were sampled roughly in proportion to their occurrence on the landscape. As it was highly unlikely that individual caecilians moved between sites within the duration of data collection, we assumed that the 400 m spacing between sites meant that each site could be considered as an independent sample. We allocated each site to one of three categories of land use: 1) agricultural land, which includes active and fallow fields as well as areas dominated by fruiting trees, 2) heavily anthropogenically disturbed land, including urban centres, habitations, school compounds and non-native pine and Eucalyptus plantations, and 3) natural, relatively undisturbed areas, including unmanaged shrubby or forested areas and the last remaining patch of Sagalla's indigenous forest. Given

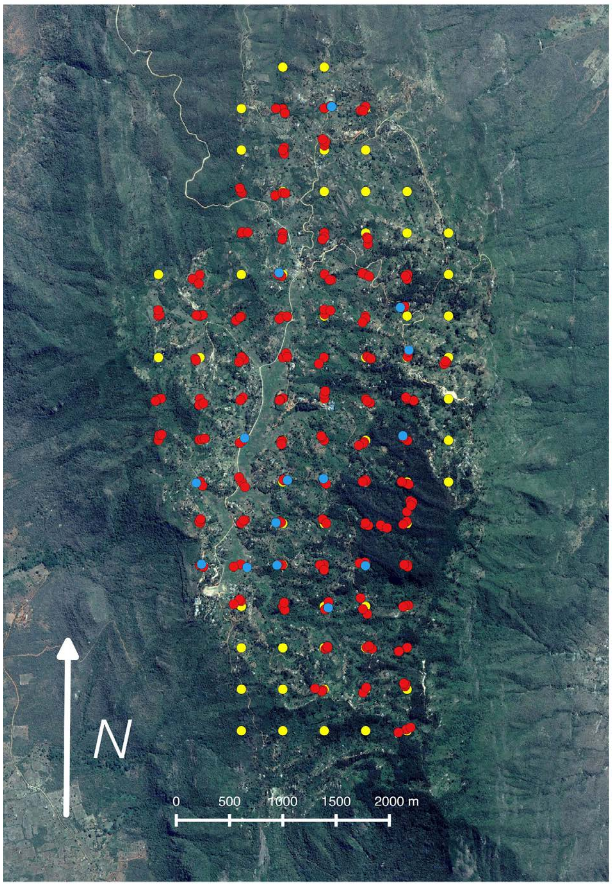

Figure 1. Sagalla caecilian survey sites, including unsampled locations in yellow, and surveyed sites in blue (caecilian present) and red (no caecilians found) on Sagalla Hill, Kenya. Note supplementary sampling in the indigenous forest habitat (darker green).

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

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

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

The second and third plot dug at each site were situated in perceived favourable caecilian microhabitat within 100 m of the GPS marker, with the exact locations selected according to the following criteria, in decreasing order of priority: 1) maximal apparent soil moisture, 2) proximity to banana plants, 3) proximity to fruiting trees, 4) maximal apparent soil fertility/organic matter content (leaf piles, cow dung). These selection criteria were based on a review of previous caecilian surveys where favourable caecilian habitat had been described (e.g. Hebrard et al., 1992; Bhatta, 1997, Measey, 2004; Gower & Wilkinson, 2005; Kupfer et al., 2005; Kouete & Blackburn, 2020). In rare cases where none of these criteria could be met, the second and third plots were dug in effectively random microhabitat exactly 30 m east and west of the GPS marker.

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

In addition to the 288 systematically distributed plots, a further 63 exploratory plots were dug using the same protocol as above, but selected opportunistically, either at sites with known historical presence (from Malonza et al., 2010), or at sites in habitat expected to be favourable to caecilians based on prior information and experience during the survey. These plots yielded additional specimens whose length and weight data added to the analysis of morphology.

Landowner survey

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

Statistical analysis

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

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

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

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

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

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

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

RESULTS

Sample characteristics

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

In total, 31 caecilians were collected in 15 of the 228 plots, representing an encounter rate of 6.6% and a catch per unit effort of 0.15 caecilians per hour. Disaggregating into land use types, plots dug in agricultural fields saw an encounter rate of 7.1% (8/112), while those dug in areas of high disturbance had 7.0% (5/71) and the natural areas were lowest with 4.4% (2/45). See Figure 1 for a site map identifying plots where caecilians were encountered at systematically selected sites. An additional 25 caecilians

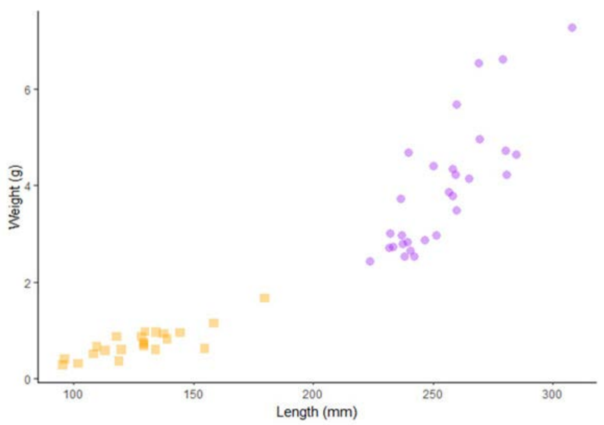

Figure 2. Length and weight distribution of specimens of Sagalla caecilian *Boulengerula niedeni* sampled in this study. Contrasting symbols and colours represent membership of the two groups identified by cluster analysis, likely representing age classes.

were captured in ten of the 63 opportunistically surveyed plots (15.8% encounter rate). Three caecilians (5.6%) were severely injured during excavation and were euthanised.

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

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

Landowner prediction survey

Of the 228 plots dug, 61.0% (139/228) were on private land, requiring that a landowner be approached for permission, while the remaining sites were located on public land. Of the 139 landowners approached, 87.8% (122/139) correctly identified *B. niedeni* from the images presented to them. Of these 122 landowners, 79.5% (97/122) confirmed that they had found the caecilians on their property before. This suggests that landowners potentially hold good information on caecilian presence. Furthermore, the encounter rate at these 97 plots where presence of caecilians were reported was 8.3% (8/97), compared with 0% (0/25) for plots on land where the owner did not report caecilians.

Mixed Effects Modelling

Of the remaining four predictors of the probability of encountering caecilians at a site, none showed any clear evidence of an effect. All models within the top set were nested versions of the top model (the null

Table 1. Comparison of all permutations of the binomial GLMM of caecilian encounter probability, ranked according to AICc, with the following covariates (variable importance, i.e. summed AIC weights of containing models, in brackets): 1 = land use type (0.11), 2 = landowner prediction (0.28), 3 = soil compaction (0.3) and 4 = surface temperature (0.46).

Covariates	df	AICc	ΔAICc	Weight
[. . . .]	2	97.5	0.00	0.230
[. . . 4]	3	97.8	0.24	0.204
[. . 3 .]	3	98.8	1.29	0.102
[. 2 . .]	3	99.5	1.95	0.087
[. 2 . 4]	4	99.5	1.97	0.086
[. . 3 4]	4	99.6	2.05	0.083
[. 2 3 .]	4	100.8	3.25	0.045
[. 2 3 4]	5	101.3	3.79	0.035
[1 . . .]	4	101.7	4.16	0.029
[1 . . 4]	5	101.9	4.39	0.026
[1 . 3 .]	5	103.0	5.51	0.015
[1 2 . .]	5	103.6	6.06	0.011
[1 . 3 4]	6	103.6	6.10	0.011
[1 2 . 4]	6	103.8	6.23	0.010
[1 2 3 .]	6	105.1	7.55	0.005
[1 2 3 4]	7	105.6	8.08	0.004

model), suggesting that they should be disregarded from consideration, and maximal importance scores were low for all variables (0.46 for soil surface temperate in the highest case; Table 1).

Density

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

DISCUSSION

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

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

The reproductive mode of *B. niedeni* is not known for certain. The closely related species *B. taitanus* is oviparous and has altricial young that are nursed via the hypertrophic skin secretions of the female (Malonza & Measey, 2005; Kupfer et al., 2006). The altricial young of *B. taitanus* have a total length of approximately 28 mm when they hatch (Kupfer et al., 2006), are unpigmented and undergo an ontogenetic shift in pigmentation becoming increasingly pigmented, with pigmentation developing from a darker mid-dorsal band which gradually broadens over time (Nussbaum & Hinkel, 1994). The young become independent of their mothers when they reach approximately 86 mm in length (Kupfer et al., 2006). Females of this species have an annual reproductive cycle (Raquet et al., 2015) and they are known to nest in January after the short rainy season (Kupfer et al., 2006). It is likely that this reproductive mode is also exhibited by *B. niedeni* and that our surveys therefore took place after the breeding and nesting season. The few juvenile *B. niedeni* that are known were unpigmented on their ventral and lateral surfaces (Müller et al., 2005), indicating that a similar ontogenetic shift in colouration also occurs in this species. The smallest individual *B. niedeni* we encountered had a total length of 95 mm and all were well pigmented indicating that animals in the smaller size class were juveniles which had already completed the ontogenetic shift in colouration. No nests were excavated which could reflect seasonality of breeding but nests might have been missed. The presence of two clear size categories of specimens which might indicate ongoing breeding as well as the presence of an annual breeding cycle like other congeneric species.

Our sampling strategy encountered a number of operational difficulties on the ground due to the inherently destructive nature of the sampling protocol. Because of the local dependence on subsistence agriculture, farmers would understandably not allow any part of their field to be dug up while their crops were sown. For this reason, many of our plots were forced away from their systematically placed GPS marker, introducing bias to the random sampling portion of the survey. This also may cause slightly sub-optimal habitat to be sampled in our first plots, as fields are often fringed by hedgerows, streams or roads. One solution to this issue could be to synchronise future caecilian surveys with the annual harvest that occurs in February in Sagalla, so that the soil is only disturbed once. Additionally, any additional caecilian mortality caused by the digging process would be minimised by sampling during a regular digging event that would occur either way, while also allowing for a greater volume of soil to be sampled. However, this might risk disturbing nests if caecilians breed at this time of year. Such a strategy should not be undertaken in habitat types that would otherwise be undisturbed until more information on the time of breeding and parental care is known. This information might be gathered by the further questioning of local land users.

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

The primary limitation inhibiting statistical analysis of the data was the low encounter rate of caecilians (15/228 plots, 6.9%). There are several ways in which future caecilian surveys could increase their encounter rate. Some avenues for future exploration include the potential use of eDNA (Thomsen & Willerslev, 2015) in the detection of caecilian presence within the soil using easily extracted soil cores. If viable, this would allow sampling without crop disruption while also shedding light on depths of caecilian activity. Secondly, a caecilian survey with mechanical digging could decrease the effort involved while increasing the speed at which the soil is removed, thus minimising the likelihood of missing individuals due to an escape response. However, mechanical excavators are expensive and cumbersome and, in many cases, including Sagalla Hill, would be unable to reach sites targeted during a caecilian survey, thus only under very specific circumstances could their superior digging power be effectively used.

The landowner prediction survey showed that most landowners were able to correctly identify the target species and that of these, 79.5% of respondents had encountered *B. niedeni* on their property before. The encounter rate of *B. niedeni* at plots where presence of caecilians was reported was relatively high and no caecilians were detected in plots where land owners did not report the presence of the species. This is consistent with landowners providing reliable reports of caecilian presence, although the small sample of absences here precludes strong conclusions on this. A limitation with our survey strategy was that we did not ask when *B. niedeni* was last seen. The climate and land use may have changed over time and once-suitable habitat may have become unsuitable. Whilst our work shows that information from local respondents may be of use in providing information on this particular species, future studies should include estimates of last sighting date. Surveys on fossorial vertebrates have a unique set of challenges, setting them quite apart from the average ecological survey of cryptic species (e.g. Gower & Wilkinson, 2005; Measey, 2006). Our ecological survey of *B. niedeni* highlighted these challenges but nonetheless produced some interesting findings to advance our knowledge of the species. We provide the first population estimate for the species which provides an important baseline for the future study of population trends overtime. Furthermore, this work supports the growing evidence for apparent tolerance for agricultural and human-disturbed habitat as well as evidence of ongoing breeding. While their apparent survival in human-disturbed landscapes may warrant cautious optimism, the species remains a narrow-range endemic, necessarily restricted to a very small area. *B. niedeni* was first assessed as Critically Endangered in 2006 on the basis of its extremely limited extent of occupancy, although it was later downlisted to Endangered (EN) in 2012 (IUCN, 2020). The current assessment is very close to becoming out-of-date. Our study indicates that *B. niedeni* probably still qualifies for being assessed as EN in accordance with the IUCN Red List of Threatened Species categories and criteria B1ab(iii) (see IUCN, 2012).

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

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