Commentary Sheet

Title: The distribution and urban occurrence of the elusive southern African hedgehog (*Atelerix frontalis*)

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I have taken into account the comments of both the examiners' reports and the pdf annotations of the external examiner.

Examiner 1

Chapter 1, Page 4, heading of paragraph 4 - *"This section of text has nothing to do with the subheading of Urban Environment."*
Page 4, heading of Paragraph 4 – changed the heading of this section from 'Urban Environments' to 'The effects of urbanisation'.

Chapter 1, Line 316 - "*This is a false statement – only A. albiventris has four, all other five species (including A. frontalis) have five. Differences in ear size and the spines characterise the different African species (see Happold, 2013)."*
Page 10, Paragraph 4, Line 3 – changed the above mentioned statement to accurately conform to literature: "*Atelerix frontalis* can be distinguished from other African hedgehog species other than underbelly colour. The ear size and spines are different for each of the African species. Specifically in regards to identification between *Atelerix albiventris* and *Atelerix frontalis*, *A. frontalis* has 5 toes on each paw, whereas *A. albiventris* have only four toes on their hind paws (Happold 2013)."

Chapter 2, Page 35, Paragraph 2 - *"Did you check the Vertebrate Red List for Swaziland? This and other publications (such as Smithers' monograph for mammals of Zimbabwe, Botswana, Shortridges's monograph for mammals of Namibia and Bulawayo Natural History Museum) should have been consulted."*
Chapter 2, Page 35, Paragraph 2 - The Vertebrate Red List for Swaziland did not list southern African hedgehogs (*Atelerix frontalis*) as one of the species native to the region. I was unsuccessful at accessing sources such as Smithers' and Shortridge's Monographs. These will be sourced for publications that arise.

Chapter 2, Discussion - *"Although the candidate took measures to prevent over-fitting of models due to skews in collecting effort towards Johannesburg and Pretoria, she should specifically address the problem of temporal and spatial autocorrelation (this term does not come up in the thesis but it is a major consideration)."*
Chapter 2, Page 24, Paragraph 2 – In the methodology section of chapter 2, steps were taken to reduce the bias present in the data, such as removing records within 1km and removing duplicates. For the Maxent modelling, I also specifically created a bias file to reduce the contribution of records in Johannesburg, Gauteng and South Africa in relation to other countries. In Chapter 2, Page 52, Paragraph 2, I also acknowledged the factors that were likely to have skewed my data collection efforts. This was added to this paragraph to consider the issue of temporal and spatial autocorrelation.

Chapter 2, Page 52, Paragraph 2, Line 8: “The influence of spatial and temporal autocorrelation could have affected the modelled outcome. While I selected fine scale climate data to reduce spatial autocorrelation, these maps represent average conditions and cannot account for the diversity of microclimates within a landscape. The climate data used were also representative of 50 years of average climatic conditions and therefore modelling efforts do not account for variations that may facilitate occurrence (Elith and Leathwick 2009).”

Chapter 2, Discussion - *“Surprisingly, future climate models all reflected a disappearance of the species in countries neighbouring South Africa which appears highly unlikely and probably reflects the paucity of recent data from these countries. This casts some doubt on the validity of the models and should be addressed.”*
Chapter 2, Page 57, Paragraph 2, Line 6 - This was considered in my study already: *“*The distribution predicted for the *Atelerix frontalis* in South Africa is an accurate representation of the possible range, although regions outside South Africa should be considered an extrapolation of the occurrence data gathered due to the limited sightings available for these regions. The multivariate environmental similarity surfaces (MESS) analysis also identified these regions as lacking sufficient information for modelling, and therefore even if sufficient records were available, better climatic data would be required in order to model the species distribution accurately (Phillips *et al.* 2006).”

Chapter 2, Discussion - *“Likewise, future models should take cognisance of the dispersal ability of hedgehogs. While future models show a range shift to include the Drakensberg range, this seems unrealistic to assume that hedgehogs will be able to disperse over these distances by 2050 to 2070. Moreover, it is also highly likely that habitat factors other than climate that prevent hedgehogs from occurring in the Drakensberg will probably persist into the future.”*
Due to limited understanding of the dispersal ability of *Atelerix frontalis*, comments regarding the species ability to move this distance is questionable. The future models should be considered as a representation of where future climates, that resemble those currently, will persist. The following statement was added to address some of the limitations in the modelling and some of the factors that may have provided for such outcomes: Chapter 2, Page 58, line 13 – “Biotic factors may have had a significant impact on the species distribution but could not be included in the distribution modelling due to the limited information for the species and the lack of available fine scale maps.”

Chapter 2, Discussion -*“Clearly ground-truthing is required, particularly in the Drakensberg as well as Zimbabwe, Botswana and Namibia, possibly targeting gardens in towns such as Bulawayo and Masvingo in Zimbabwe and Windhoek Namibia. A more standardised, useful census method, particularly in rural areas, could be the use of road transects to detect road kills. It would be interesting if the candidate could indicate whether hedgehogs have been recorded in such southern African road kill surveys…. Other monitoring techniques which could be recommended include radio-tracking, camera traps and footprint tracking.”*
Chapter 2, Page 58, Line 16-20: These sentences address the clear need for ground truthing to validate the models used but also explains the difficulties in doing so, such as time and cost. Currently, I do not have information addressing future studies. In my study, some hedgehogs reported were road kill incidents but aside from those I collected directly from the public I was unable to find any road kill surveys that mentioned hedgehogs. Even in my communications with Wendy Collinson from EWT, citizen science and active survey road kill project, there were no reported sightings.

Chapter 2, Page 58, Line 18 – This was added to the current sentence to address the future studies that could be implemented for the species: "Future studies should aim to assess aspects of the realised niche through, for example, resource selection at a local scale, road transects, radio-tracking, or camera traps."

Chapter 3, page 70, Paragraph 1, line 2- *"The statement about 'small non-significant differences in odds' for Joburg is contradicted by the graph that shows significant (*) differences at most of the intervals?"*
The * assigned to each distance category, soil or vegetation type indicates significant difference in relation to that specific category and not relative to the other categories. It is more an indication whether the group had both presence and available data and whether there was a significant difference between the presence and available data in that category. I added this to the title of each log odds ratio graph to explain this more explicitly: '* = $p < 0.05$ for presence vs available data in each category.'

Chapter 3, Page 82, Paragraph 2 - *"Is this not an arbitrary function of the fact they were identified from road kills or road sightings due to higher detectability here compared with areas away from roads?"*
The examiner is questioning the validity of stating that roads may act as a resource. However the detectability issues raised where addressed later in this section Chapter 3, Page 83, Paragraph 1, Line 4: "Sightings of *Atelerix frontalis* in vegetated areas are rare, due to their nocturnal activity patterns and camouflage provided by their tawny coloured spines, which blend into the grass (Smithers 1983; Skinner and Chimimba 2005). The majority of the sightings reported are of *Atelerix frontalis* crossing roads, entering private property and/or being caught by dogs. Some sightings of *Atelerix frontalis* were also related to road kill incidents, typically on busy highway roads in South Africa or Johannesburg, in areas bordering undeveloped land. *Erinaceus europaeus* have similar sighting patterns (Hof 2009; Haigh 2011)."

Chapter 3, Page 86, Paragraph 2, Line 3 - *"Can you really say this given different classifications used and bias sampling?"*
I added the following to the final conclusion of chapter 3 to address the issues regarding the differing sampling. The soil maps used for the large and fine scale analysis were the same and the biased sampling issue was addressed in chapter 2. Chapter 3, Page 84, Paragraph 2, Line 3-7: 'It appears that *Atelerix frontalis* are inhabiting more nutrient rich soils at a large scale while at a fine scale occurrences were predominately in nutrient poor and less agriculturally desirable. I hypothesize that the observed difference in soil selection is related to *Atelerix frontalis* displaying behavioural plasticity through niche differentiation.'

Chapter 3, Discussion - *"The significant biases in the data may render conclusions based on this approach somewhat arbitrary and speculative. Since the citizen science records are skewed towards cities, roads, gardens and parks, this means that results reported reflect differences in detectability rather than actual occurrence. This needs to be clarified by the candidate."*
This was addressed in the discussion section of Chapter 3. Page 83, Paragraph 2: 'The proximity of *Atelerix frontalis* to anthropogenic features is likely to be an indicator of where people are most likely to encounter hedgehogs, particularly when the species inhabits the surrounding vegetation. In support, the odds of *Atelerix frontalis* occurrence in South Africa were highest in close proximity to four anthropogenic features but only one natural feature (stagnant natural water sources). The Johannesburg scale analysis also revealed no difference

in odds of occurrence in relation to any of the features analysed, except roads. In order to confirm the resources used by *Atelerix frontalis*, fine scale analysis of home range and activity patterns will be required.'

Chapter 3, Discussion - *"Another aspect that seems speculative concerns comparisons of the RSF results at local and national scales leading to the conclusion that niche differentiation have resulted from hedgehogs invading the urban niche. Apart from sampling biases, the different vegetation and soil coverage used at different scales and inconsistencies in spatial datasets used at national and local scales, must render the results from different scales as being not directly comparable. The "urban bias" would apply to the Joburg scale but not as much to the national scale."*
Added a section to the conclusion of chapter 3 to address this issues. Page 86, Paragraph 2, Line 13: 'Some consideration needs to be taken into account for the use of different vegetation maps and scales for the resource selection analysis. The difference in resource selection may be attributed to spatial differences in the South African landscape but given that nutrient rich soils were available in the Johannesburg area and not occupied, it appears that another factor may be at play.'

Chapter 4, Discussion - *"The expectation of a limited breeding season based on torpor and published breeding data are not born out of the data which show presence of juveniles throughout the year. This discord was not adequately addressed in the thesis. Perhaps given the provision of food in an urban context, hedgehogs in Joburg do not need to undergo torpor?"*
Page 94, Paragraph 1, Line 5: 'The sustained presence of *Atelerix frontalis,* especially juveniles, throughout the year may bring into question whether torpor occurs in the urban environment and the limited seasonal breeding of the species. However, research on *Atelerix frontalis* torpor patterns indicate that changes in temperature and photoperiod are the factors regulating activity (Gillies *et al.* 1991). The provision of food resources appears to have no effect on torpor as even pet hedgehogs have been reported to enter torpor during winter. The continuous juvenile activity, especially those found in winter, appeared to be related to inexperienced youngest that selected unsuitable nesting sites which resulted in contact with people. The large grouping of juveniles and sub-adults could also be a result of non-standardised approaches of measuring age at FreeMe Rehabilitation Centre.'

Chapter 5, Page 99, Paragraph 2 - *"Seems very speculative given different sampling biases at different scales. Also did you not use different categories of vegetation variables (at least for soils and vegetation) for Gauteng and national scales?"*
The issues regarding the differing scales and use of maps were addressed on Page 86, Paragraph 2, Line 13. Also I changed the wording in this sentence to specifically draw connections between the soil characteristic differences: The Page 97, Paragraph 2, line 1: 'The Johannesburg *Atelerix frontalis* population appears to be selecting for different soil resources than the large scale *Atelerix frontalis* population.'

Examiner 2

General comments from examiner were taken into account. I reviewed my dissertation and corrected inconsistences, formatting issues and the use of species scientific name in figures and tables.

Chapter 1, Line 59 - *"Consequences of what? Be more specific."*
Page 2, Paragraph 2, Line 2 - Added clarifying statements to be more specific about the consequences that are relevant: 'Gaining knowledge about the effects of environmental change on species and predicting future consequences **of habitat and environmental change** is essential to determine which species are the most threatened and are of immediate conservation concern (Dormann 2007; Thomaes *et al.* 2008; Jackson 2011).'

Chapter 1, Line 160 - *"To what? Be more specific."*
Page 5, Paragraph 3, line 3- Added clarifying statements to be more specific about the species adaptive capacity and resilience: 'The vulnerability of a species is dependent on its resilience and adaptive capacity **to climatic and anthropogenic environmental changes**.'

Chapter 1, Line 166 - *"Give an extra line about edge effects."*
Added an additional sentence about edge effects, Page 6, Paragraph 2, Line 1- 'Large geographic ranges help to reduce the impact of environmental change on species**. The areas that are often first to be affected by environmental change are the edges of the species distribution. Edges are characterised as regions where the ecosystem structure and composition begin to change, such as transition zones between habitats (**Dickman and Doncaster 1987). These edge effects are less prominent for large source populations because more area is available to occupy, even when some parts of the geographical range become unsuitable (Robinson *et al.* 1992; Williams *et al.* 2008).'

Chapter 1, Line 178 - *"I found this section was a bit confusing to read. First before you talk about niche differentiation, you need to provide more context on what a niche is, the difference between fundamental and realised niche. Then provide some background on niche differentiation and phenotypic plasticity, and then you can finish off with adaptive capacity" and "Explain niche theory better."*
Added these sentences to the section to provide better introduction. Page 6, Paragraph 3 – 'Every organism contributes to ecosystem functioning and the specific ecological contribution are based on the species behavioural, morphological and physiological adaptations. The interaction between a species and its environment, both biotic and abiotic, is known as a niche (Peterson 2001; Thomaes *et al.* 2008). A niche can be broken down into two parts for each species. The fundamental niche is the region a species can occupy if there were no limiting factors, such as predation, food or mate availability (Peterson 2001; Thomaes *et al.* 2008). While the realised niche is the actual area a species occupies in the environment due to interactions with the ecosystem (limiting factors) (Peterson 2001; Thomaes *et al.* 2008).'

Chapter 1, Line 189 - *"Put this section on niche differentiation and the next on phenotypic plasticity first in this section. As it stands the reader needs more introduction before you get into it."*
Moved section to the beginning of this section. Page 6, Paragraph 4.

Chapter 1, Line 286 - "*Put this sentence in previous section to provide context. Otherwise I was wondering why you were telling me about the European Hedgehog."*
Page 10, Paragraph 1, Line 1 - I moved this sentence to the end of the European hedgehog section. To give it better flow to the next section.

Chapter 1, Line 286 - "*Add the full distribution that you have on the poster."*
Current IUCN distribution map added to Page 10.

Chapter 1, Line 290 - *"Use a more local term rather than steppe."*
Changed to Page 10, Paragraph 2, Line 2 -"*Atelerix frontalis* are primarily found in the savanna and grassland biomes, showing a preference for temperate and dry grassland or savanna, tree savanna and subtropical dry forest regions (Skinner and Chimimba 2005)."

Chapter 2, Line 1 - *"This chapter isn't on SDMs in general, it is of SDMs on the SA hedgehog. So be more specific in your title. Similarly, the introduction and 'lit review' needs to encompass more than just the different types of models" and "Intro needs work for chapter 2 to set the scene better. Not only an intro about SDMs needed, but also better motivation on why you are doing them for hedgehogs. In the other data chapters you have good introductions that set the scene well, so do this for chapter 2."*
Added this to the introduction section of chapter 2 to create better flow. Page 13, Paragraph 1 - 'Protecting species for the future is an important part of preserving biodiversity, but without accurately determinng species distributions, conservation efforts may be unsuccessful (Anderson and Martinez-Meyer 2004; Thomaes *et al.* 2008). Elusive species such as *Atelerix frontalis*, where only a few occurrence records are available and the distribution has not been well established, species distribution modelling can greatly aid in determining the likely distribution of the species and possibly find previously unknown populations (Pearson *et al*. 2007; Thomaes *et al.* 2008; Jackson 2011). Species distribution modelling is an invaluable tool for establishing a species fundamental niche and a platform to investigate the species' realised and ecological niche.'

Chapter 2, Line 58 – *"What does this mean for the type of data needed? Does it need more environmental variables? How robust is it for rare or abundant species? Presence or absence data?"*
Page 16, Paragraph 2 – 'Due to the limited biological information available for *Atelerix frontalis*, I could not limit my study to one modelling method or evaluate the characteristics of each model for best fit. Each mathematical model that has been designed for SDMs provides for differing relationships between a species and the environment. These relationships can be complex or simple depending of the species physiological tolerances but when there is a lack of depth knowledge of a species, it is recommended that multiple modelling methods are used to cater for numerous possible relationships (Miller and Franklin 2002; Pearson 2007; Elith *et al.* 2008; Phillips and Dudik 2008).'

Chapter 2, Line 102 - *"The review of each type of modelling technique is lacking. It does not come through clearly that you are aware of the advantages and disadvantages of each type. Go intro more detail, review when they have been used, how successful were they? How well is each suited to hedgehog data?" and "You need more detail about the different types of SDMs, as well as examples of when they've been used and when they are most appropriate."*

The advantages and disadvantages of each model were addressed in text: BRT – Page 14, Paragraph 3, Line 8. GLM – Page 15, Paragraph 1, Line 7. Maxent - Page 15, Paragraph 2, Line 3. NN – Page 16, Paragraph 1, Line 3.

Chapter 2, Line 112 - *"These aren't really prediction. They are just four different outcomes. A prediction would be based on expert knowledge and would you be choosing which of these four outcomes is most likely? So either reword or choose one."*
Changed the wording of the sentence to reflect recommendation. Page 16, Paragraph 3, Line 7 – "Possible outcomes. Considering the effects of climate change and increasing anthropogenic development in many areas of southern Africa, **there are** four possible outcomes modelled for the changes in the *Atelerix frontalis* distribution."

Chapter 2, Line 243 - *"Why is replication an issue? Be specific about what you mean."*
Added to Page 21, Paragraph 1, line 3 – 'Replication is an issue in occurrence data as it could be the result of duplicate records of the same hedgehogs and limiting sightings to the 1 km^2 radius reduced possible sampling bias.'

Chapter 2, Line 261 –*"Why is this important?"*
Page 23, Line 2 – "Knowledge of the QDSs where *Atelerix frontalis* were once seen and have not been seen again, can provide important information about the species distribution patterns, changes in the past and aid in understanding the possible future distribution."

Chapter 2, Line 270 - *"Why? They're only 100 years apart. You haven't given motivation as to why they wouldn't represent the present distribution." And "Unclear why you split records by date (post 1980 into decades) but then model them all together."*
Added information to clarify this statement, Page 23, Paragraph 2, Line 9: 'Given that the species has a life expectancy of only 3 years, many generations could have existed over the 100 year period and may not be representative of the current generation (Skinner and Chimimba 2005). Data were split into these categories to account for changes in the frequency and distribution of sightings.'

Chapter 2, Line 350 - *"What is the ecological significance of these variables?"*
Added to Page 25, Paragraph 3, Line 13 - 'Due to the lack of information available for the physiology of *Atelerix frontalis*, several variables that were unrelated to each other were used to account for the possible influences on species occurrence.'

Chapter 2, Line 402 - "*What do all of these mean?"*
Added to address examiners remarks. Page 29, Paragraph 2, Line 3 – 'BRT mathematical models resemble trees, where branches represent different decisions and leaves represent the final outcome. In a BRT tree, complexity is a function that decides on the number of branches, the learning rate is the speed at which the equation stores mathematical relationships and the bag function is the contribution assigned to initial poor fitting decision trees (Elith *et al.* 2008; Elith and Leathwick 2009). BRTs modelling follows the approach of making numerous trees one at a time where each tree corrects for the failures of the last.

Chapter 2, Page 37, Figure 2.7 - *"Logically though this distribution map looks a bit off. Does it make ecological sense to divide the two? Are these two populations or meta-populations?"*

The two quarter degree role was followed in creating the map in question and in the discussion I explained that this outcome was more likely to be related to lack of information in the areas rather than distinct populations. Page 53, Paragraph 3, Line 4.

Chapter 3, Page 59 - *"I would change this to large scale, and then say fine scale instead of urban scale. Urban is not a spatial unit of scale, it's a classification of settlement density and economics."*
I corrected the terminology throughout this section to refer to the South African scale analysis as the large scale and the Johannesburg scale to be the fine scale.

Chapter 3, Page 61, Figure 3.1 – *"Can you not maybe recreate the Johannesburg figure in this composite? Get the shapefiles and have it all in the same format. The resolution on the Johannesburg image is poor and detracts from the graphic."*
Updated the figure in question to ensure quality was of a better standard than previously and is no longer of poor resolution.

Chapter 3, Line 75 - *"South African or southern African? As you have defined as the meaning of SA."*
Page 61, Paragraph 1, Line 9 - The reference to SA Biomes in the text was the name of the file used, so I updated the sentence to have inverted commas to indicate it is a name. Previously, the shortened name I had given to the southern African hedgehog was SA hedgehog and this brought about confusion regarding the meaning of SA. However, on the recommendation of the examiner all references to SA hedgehog were changed to the species name *Atelerix frontalis* and this corrected for the confusion.

Chapter 3, Line 76 - *"Why didn't you use Mucina and Rutherford for the whole of South Africa instead of just using the biome map?"*
Added to text to clarify Page 62, Line1- "Different vegetation maps were used for large and fine scale analysis because the detail required for the large scale analysis was too limiting for the fine scale analysis (all the sightings were in one vegetation type) and the detail required for the fine scale analysis would have resulted in too many categories to draw a meaningful conclusion are the larger scale."

Chapter 3, Line 126 - "*Why is this in quotation marks? Also redefine as it has not been mentioned in this chapter."*
The sentence was modified to define glm and function was taken out of quotation marks. Page 63, Paragraph 2, Line 15 – "Data analyses were done in R version 3.1.2 and because the data were over-dispersed, the generalised linear model (glm) was run with a quasipoisson function."

Chapter 3, Line 379 - *"Look at the following references on bias in collecting distribution data. While hedgehogs might use roads etc. They might also be spotted more here because that's where people are… include in the discussion. Botts et al 2011. Geographic sampling bias in the South African frog atlas project: implications for conservation planning. Biodiversity Conservation, (20): 119-139." And "I would like you to be more critical of your results in the discussion though with regard to where hedgehogs are seen versus where they occur. I know this is a data limitation, but be aware, for example, that in the Greater JHB region there are not many areas at all greater than 10 km from a road. And if there are, it is unlikely people would be there in high densities/see the hedgehogs."*

The examiner is questioning the validity of stating that roads may act as a resource. However the detectability issues raised where addressed later in this section Chapter 3, Page 83, Paragraph 1, Line 4: "Sightings of *Atelerix frontalis* in vegetated areas are rare, due to their nocturnal activity patterns and camouflage provided by their tawny coloured spines, which blend into the grass (Smithers 1983; Skinner and Chimimba 2005). The majority of the sightings reported are of *Atelerix frontalis* crossing roads, entering private property and/or being caught by dogs. Some sightings of *Atelerix frontalis* were also related to road kill incidents, typically on busy highway roads in South Africa or Johannesburg, in areas bordering undeveloped land. *Erinaceus europaeus* have similar sighting patterns (Hof 2009; Haigh 2011)."

Chapter 3, Line 399 - "*Grasslands are also the most threatened biome inn South Africa. Find a reference for that."*
Page 84, Paragraph 2, Line12 – 'In particular, grasslands are the most threatened biome in South Africa as they are commonly used for agricultural, mining and industrial activities as well as support majority of South Africa's population (Scholes 1997; Neke and Du Plessis 2004).'

Chapter 4, Line 140 - *"I find this sentence a bit confusing. Please clarify."*
Sentence was clarified Page 94, Paragraph 3, Line 7 – "Some *Atelerix frontalis* have been known to enter private property in order to gain access to pet food, but the majority of individuals appear to be sustained by the natural environment because they are in good body condition prior to coming into contact with people (Lynch 1983; Smithers 1983)."

Chapter 5, Line 58 - *"What is it due to then?"*
Sentence updated, Page 97, Paragraph 3, Line 6 – "The actual area occupied (realised niche) by the species is often more due to ecological (i.e. competition and resource locality) and anthropogenic factors (human influences) than due to the climatic factors (Dickman and Doncaster 1987; Peterson 2001; Thomaes *et al.* 2008)."

Chapter 5, Line 95 - *"Use this reference here: Botts et al 2011. Geographic sampling bias in the South African frog atlas project: implications for conservation planning. Biodiversity Conservation, (20): 119-139."*
This reference was added to the sentence, Page 98, Paragraph 3, Line 8 – "These features are likely to indicate of where people live and conduct common activities (Botts *et al*. 2011) and which increase the encounter rate with *Atelerix frontalis*, which are elusive and sightings are rare."

Chapter 5, Line 136 - *"This paragraph comes out of nowhere. Either include a linking sentence or a subheading."*
Sentence was moved to address the next comment and updated as follows. Page 100, Paragraph 2, Line 17 – 'Future studies would do well to sample rural areas and non-affluent demographics as my research primarily targeted English speaking individuals with access to computers and therefore skewed my sampling efforts.'

Chapter 5, Line 157 - "*Move the section on sampling affluent English speakers to here. You can include all these recommendations under a sub-heading of recommendations for future studies."*
Moved and addressed as stipulated in the above comment.