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Population and life history characteristics of coexisting small mammal species in a grassland habitat

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Response to comments for Jennifer Lancaster, PhD thesis: Population and life history characteristics of coexisting small mammal species in a grassland habitat

External 1 (1 page comments):

*The examiner suggested reading "Ribble, D.O.; Perrin, M.R. (2005) Social organization of the Eastern Rock Elephant-shrew (*Elephantulus myurus*) : the evidence for mate guarding Belgian Journal of Zoology 135 (supplement) : 167-173" and also some more papers by Rathbun to further explore why sengis as so unqiue.*

** These revisions have been done throughout.

It was also suggested that I explore the recent phylogenetic history of afrotheria (and sengi's).

I have included this in the introduction under the subheading "The rock sengi, *Elephantulus myurus*".

** The distinction between scrotal and non-scrotal *E. myurus* has also been made clear.

Pg 3, line 6. Should be "where" not were

** Done.

Pg 15, line 9. (now pg 16) *Kalcounis-Rüppell & Millar was not a study in a desert ecosystem.*

** Changed.

Pg 23, lines 24 – 25. (now pg 24)*Hunter, not hubter; and delete extra "be".*

** Hunter changed; couldn't find extra "be".

Pg 29, line 20. (now pg 30) *Insert but before differences.*

** I feel it reads fine, the comma acts as a separator rather than putting a "but" in which may change the meaning of the sentence.

Pg 31, description of density calculation. (now pg 32) *I am not clear at all how density was determined from 490m^2? Please elaborate.*

** Done.

Pg 38, Figure 3.4. (now pg 39)*The legend is not clear at all.*

** Done/Changed.

Pg 39, 2nd line from bottom. (now pg 40)*Misplaced parentheses.*

** Changed.

Pg 41, last paragraph. (now pg 43)*This reference from French implies that sengis are insectivores, which they are not. This should be changed.*

** Done.

I think this might be due to the fact that when the reference was written, sengi's were still classified as part of the insectivore.

Pg 48, line 11. (now pg 49) *Misplaced parenthesis with Nilsen reference*

** Changed.

Pg 52, line 10. (now pg 53) *This sentence imples to me that* E. myurus *defend territories in, or as a pair. This is not the case as indicated by Ribble and Perrin.*

** Modified after reading Ribble and Perrin paper.

Pg 59, removal experiments. (now pg 60) *I am amazed that by removing individuals on 200m, that no individual returned.*

** I have clarified this now – removal individuals were placed on another grid at least 1km away from any other grid and monitored for signs of re-establishment. The only movement between removal grids and the control grids was the occasional (literally 3 or 4 individuals) male *Michaelamys namaquenis* which would be found as non-scrotal on one grid in one trapping session and then as scrotal on another grid in a subsequent trapping session. I assumed this was dispersal from the natal area.

Pg 82, line 14. (now pg 83) *Kalcounis-Rüppell & Millarwas about* P. californicus *and* P. boylii, *not* P. eremicus.

** Changed.

External 2 (4 pages of comments):

The examiner comments on the lack of reference to the phylogenetic histories of the species concerned as this may affect the degree of competition.

** This has been corrected, especially for *E. myurus*, to show how different sengis are.

The examiner also comments on the lack of broad ecological and behaviour theories.

** I tried to focus my writing on the relevant information, rather than writing a large literature review with information that was not directly pertinent to the current study.

There are comments regarding the use of "probably" in the discussion section and "competition" throughout.

** I have tried to correct this as far as possible by more clearly defining what I mean by competition and reducing the use of the word probably.

Pg 8, line 14. "Three types" specify.

** Done.

Pg 12, line 18. "… both species are restricted to rocky outcrops…" Where? This study? Elsewhere? Any other species found? Habitat definitions?

** Expanded and clarified - but in terms of where the species were caught, concurrent trapping studies were done in the surrounding grassland at the beginning of the study. However, trapping success was incredibly low, and only one *Elephantulus myurus* and a couple of *M. namaquensis* were caught in the grasslands. Despite ongoing trapping, these individuals were not re-trapped. Additionally, very few individuals of other species were caught on rocky outcrops. This is not mentioned in terms of the thesis itself due to the rarity of such occurrences which decreases the importance of such trappings.

Pg 14, line 8 (now pg 15) *"…additionally…" and what follows can be confusing. Recommend changing to "however"*

** Done.

Pg 16, lines 14 – 15. (now pg 17) *Microhabitat selection – definition especially in terms of spatial definition vs environmental factors affecting behaviour.*

** Clarified.

Links to pg 82, 4th last line (now pg 83). *“.. Microhabitat patterns were not clear”.*

** Clarified.

Pg 21, Discussion, 1st sentence (now pg 22). *State how rainfall may influence diet composition and quality.*

** Done.

Pg 21, last sentence (now pg 22)*: “…probably reflects the availability” – as this was not measured, “could” would be safer.*

** Done.

Pg 24 2nd last paragraph, last sentence (now pg 25). *How is microhabitat selection partitioned?*

** Clarified.

Pg 39, 5th line from bottom (now pg 41). *“Surprinsingly” regardless of method, the density of the generalist… was always higher than that of the specialist. The generalist as a rodent is primary consumer whereas the sengi is secondary consumer and thus this is expected in terms of trophic levels.*

** Expanded explanation.

Pg 42, lines 21 – 22. Again “probably”. However, as both species co-occur, the “unpredictable environment” would have an impact on M. namaquensis*, as well; both r – and K-selected species are present.*

** I can’t seem to find this in order to clarify it!

Pg 46, lines 6 – 7 (now pg 47). *“Widespread” is a measure of spatial distribution, while “territorial” is a behavioural measure. Thus widespread does not equate with territoriality.*

** Redefined.

Pg 50, line 12. Insert “identity” after “species”.

** Done.

Pg 61, 2nd last line (now pg 63). *Perhaps “… early rainy and late rainy seasons...” would be more accurate.*

** Done.

Pg 72, line 5 (now pg 73). *“similar sized” In all other chapters* E. myurus *is slightly larger than* M. namaquensis.

** Corrected.

Pg 72, line 10 (now pg 73). *"high degree of resource overlap" rather use "high degree of overlap in resource use"*.

** Changed.

Pg 73 (now pg 74). *It is not clear why experiments were conducted on a "neutral" outcrop. If they were staged in a neutral arean, presumably the individuals were transported to and from the lab to this outcrop. Could this have caused some stress?*

** Neutral rocky outcrops were used to decrease the effect of the dear-enemy phenomenon as explained in the introduction and discussion of this chapter. Basically, if you know your neighbour, you are less likely to be aggressive to him in familiar areas. Additionally, the rocky outcrop was probably 20m from where the animals were kept overnight in order to keep stress to a minimum.

Pg 74, 5th line of results (now pg 75). *If, in general,* E. myurus *was slightly larger than* M. namaquensis*, why now significantly heavier? Especially as individuals were chosen at random?*

** When looking at overall population trends, *E. myurus* was not significantly heavier than *M. namaquensis* as was shown in the life history chapter. However, due to pure chance, and also possibly the requirement of not re-using individuals more than necessary, in the behavioural studies, *E. myurus* were heavier than *A. namaquensis*.

Internal:

The examiner had comments about:

Broad Ecological concepts:

** The examiner commented extensively in the comments on how coexistence may occur. Although not dealt with in as much detail as the examiner in terms of the how species coexist, the concept of evolutionary vs ecological time scales in coexistence (explanations 1 – 3 in the 2nd paragraph) is dealt with under the heading "the importance of coexistence" in the introduction. In order to address the 4th explanation regarding phylogenetic differences and the fact that the species are different, I have included a section of the phylogenetics of especially *E. myurus* and the macroscelidae in the introduction. Already in the introduction is an explanation of how co-existence is frequently studied in larger mammals of different orders. Additionally, throughout the thesis, but especially in the 2nd chapter, I provide evidence for a large amount of overlap in resources between the species which implies that there is a need for mechanisms to promote coexistence while possibly reducing competition.

Evaluation of interspecific competition:

** I have evaluated interspecific competition using references regarding small mammals throughout the thesis.

Reporting of raw data in figures:

** In terms of behavioural studies, it is conventional to present data in the format that it has been presented as it allows for meaningful comparisons without too much manipulation so that the data fits a theoretical model. As all chapters have been written in draft paper format and this is the conventional method of presenting data, it allows for easy comparison.

Writing quality:

** In terms of writing quality, where other examiners have expressed concern over clarity, corrections have been made. Additionally, a 3rd party has read through the thesis and commented on any places where logic appears incomplete.

Use of statistics and p-values:

A comment from Pg 50. Throughout the thesis, statistics about the model fit should be reported. Also there are places were a significance of interaction is reported but not included in the analysis.

** The examiner makes many valid points regarding the statistical analyses of my thesis. Firstly, after some statistical advice and literature search of other similar studies, I felt it was not necessary to report statistics about the model fit. Additionally it is not conventional in behavioural ecology with no modeling. Also, current statistical feeling is that 2nd order effects are more important than 1st order effects. However, I have presented both. Furthermore, I feel that the analysis I have done sufficiently answer the questions I was asking. I will however consider making some of the changes proposed when submitting papers for publication. Unfortunately, many of the useful suggestions will be difficult to implement due to some small sample sizes due to relatively low trapping success. I realise that a strict alpha level is no longer recognized, but there needs to be some sort of cut off. To this end, those values that approach significance are described as trends throughout the thesis while those that are significant with no clear trends are explained as such with possible reasons for these findings.

Pg 14 (now pg 15). *Use of the word "habitat" – suggest environment, biome, vegetation community, patch type.*

** I agree that for an ecological publication, habitat may not be suitable and patch (which implies smaller area) or biome (the study site is right on the border of grassland-savanna biome) might be better. However, for the purposes of my study, I feel habitat, as a descriptor of the greater area, is appropriate.

Pg 15 (now pg 16). *Sentence ending with "…or extrinsic factors depending on spatio-temporal availability" is unclear/irrelevant.*

** Clarified.

Pg 15 (now pg 16). *Sentence beginning with "These changes may be in space... " is unclear/irrelevant.*

** I'm attempting to set up a base on which to build some of the ideas.

Pg 16 (now pg 17). *Rephrase the predictions as testable research hypothesis*

** Clear hypotheses and aims are provided in the introductory chapter. Thus testable predictions are used in the chapters – a hypothesis or aim can be easily reconstructed from this. I have however reworded them as hypotheses.

Pg 17 – 18. (now pg 18)*There are more appropriate ways to analyse these data such as a logistic regression. With the discriminant analysis – what is being discriminated and why are the species analysed separately when they are being compared?*

** General Discriminant Analysis was used to see if either species significantly associated with any particular microhabitat variable that was measured. If there was a significant relationship in one species, it was compared to the alternative species as if both are associated with a particular feature, the potential for competition increases. A logistic regression will be considered in publications.

(now pg 19) *Diet overlap and indices need investigation/clarification, especially some detail on the indices, the range of possible values and what it means biologically.*

** The biological significance of the results is reported in the results and discussed in the discussion. As it is a percentage value, the range is from 0% (no overlap) – 100% (high overlap) – this is discussed in the results/discussion. As the chapter, and subsequent publication, are not dealing with the assumptions of the model, but rather using the equation as a means of comparison and evaluating overlap, not only within this study, but also between studies, I feel that to go into details about the indices and how they are derived would be irrelevant.

Pg 20 (now pg 21). *Fig 2.2. is a line graph for categorical data - a bar graph is more appropriate*

** A line graph was used to show seasonal trends clearly, which was not as visibly clear with a bar graph

Pg 30 (now pg 31). *The aims should be rephrased as testable research hypotheses. How do differing life histories contribute to coexistence between* M. namaquensis *and* E. myurus*?*

** Clear hypotheses and aims are provided in the introductory chapter. Thus testable predictions are used in the chapters – hypotheses and aims will be re-inserted in publications.

Pg 32 (now pg 33). *Revision of terms is needed here: "Emigration" (=dispersal) which already has a well-established meaning in ecological literature, "loss" (= emigration and death) may be more appropriate. Also "survivorship" and "survival" are not the same thing – I recommend "persistence".*

** Corrected and clarified.

(now pg 34) *How was sexual dimorphism measured (difference, ratio?)*

** Clarified.

(now pg 33) *Fig 3.1. has interesting information that should be included in the results*

**Fig. 3.1. was merely used as an illustration on how adult/juvenile weight was calculated. Of more importance/relevance to my aims (i.e. do differences in life histories promote coexistence) is when juveniles appear in the population and when individuals are reproductively active and when they aren't, which is presented in the results. Also, as these are draft papers, only one figure was included. However, the figure for *E. myurus* appeared very similar with the cross over point at around 49g rather than 38g as for *M. namaquensis*.

Pg 33. (clarified on pg 32) *Use of J-S and MNA – I've never heard of MNA. Details of the models needs to be included – how was it used, what software was used to fit the models? How were the models tested? How did you test the assumptions?*

** MNA is a standard method used in small mammal studies, but is sometimes also called MNKA – I have included this information the first time I mention MNA. I have included a reference to why the different methods were both used in the methods section. Additionally, in the text, it was explained why there were such great differences and why I selected MNA as a more reasonable estimation of abundance.

(now pg 34) *Tests of skewness, normality etc – what do they tell us about the biology?*

** Clarified.

Density vs population growth rate – there is mention in the methods but I see nothing in the results. Analysis should be focussed on comparisons between growth rates of the species as density is a bad measure of life history differences. We want to know which species can increase more quickly when conditions become favourable?

** Density vs. population growth rates. Firstly, I couldn't find this reference. However, as density is intrinsically linked to life history strategy (i.e *r*-selected or Type I species will have unstable population densities due high reproductive rates and turnover, whilst *K*-selected or Type III species will have more stable population densities due to lower reproductive rates but higher survival), a comparison of densities is suitable. Although I agree with the examiner that it would be good to know which species can increase more quickly when conditions become favourable, due to phylogenetic constraints and the species biology, it is unlikely that *E. myurus* will increase numbers dramatically when conditions improve while *M. namaquensis* is

likely to do this. Thus a comparison of densities and how this may affect competition and hence co-existence is more suitable in this case.

Pg 34 (Clarrified on pg 32). *There are large differences between MNA and J-S which raises concerns. Which is more appropriate?*

** I refer to my response for a comment above (pg 32). In the text, it is explained why I got such differences (based on the assumptions of the models), and why I decided to use MNA over J-S.

"Skewness" must be translated into biology. What period is used to establish skew?

** Clarified the use of skewness in the methods (pg 34).

Pg 35 (now pg 36). *Fig 3.2 should be a bar graph which is more appropriate for categorical data*

** A line graph was used to show seasonal trends which is not clearly visible on a bar chart.

Pg 36 (now pg 37). *Fig 3.3 should be a bar graph. The patterns would be easier to see if the sexes were separated and the percentage, rather than the number were reported*

** A line graph was used to show seasonal trends which is not clearly visible on a bar chart.

Pg 39 – 40 (now pg 41). *There is a prediction at then end of pg 39/beginning of pg 40 that could be tested using numerical responses.*

** I am providing a possible reason for the trends I found. Optimal conditions for the species may vary, thus affecting the numerical responses.

Pg 45 (now pg 46). *The term "spatial organisation" is vague. The chapter is about home range use – would that term not be better? A definition would help.*

** Spatial organization is a standard term in behavioural ecology describing not only home ranges but how differences and similarities in home range use and overlap affect and may be affected by interactions between individuals.

Pg 48 (now pg 49). *Because of the importance of accurate home range size estimation, some assessment of sample size is necessary. For MCP, it is usual to plot a figure to define "enough". I doubt 4 locations/animal would be sufficient.*

** I agree with the examiner. However, due to low trapping success, I had to use whatever data were available.

(now pg 49) *Also, in other species, home ranges differ markedly across seasons.*

** For the same reason as given above (small sample size), data could not be analysed across different seasons, nor could the effect of grid be separated out.

(now pg 49) *Description of the methods requires more detail e.g. how were overlapping individuals chosen for observation? What was the standard for inclusion in the movement analysis?*

** If an individual overlapped, it overlapped. However the percentage of overlap varied as home range sizes were not consistent, so although there may have been some non-independence of samples, I do not feel that it made a significant impact on my results. Additionally, biologically, which value of overlap is more important – the larger or the smaller? As personality, which affects home range use and overlap, as well as temporal overlap (in terms of activity in the same place at the same time) is unknown, both values need to be considered.

(now pg 49) *"the percentage home range overlap was calculated" belongs in the methods.*

** Corrected.

Pg 49 (now pg 51). *Fig 4.1. needs some clarification.*

** Clarified

Pg 50. How was non-independence of movement distances dealt with? This would call for a mixed-effects model. There are some issues with the reporting of "no effect" – one can only conclude that no effect was detected, not that the effect was absent. If no effect was important, a power analysis would be needed.

** Conventionally, a mixed-model effect would be used. However, due to a low capture rate, there are not enough degrees of freedom for a mixed effects model as the number of categorical predictors exceeds the sample size and thus the degrees of freedom would be compromised. With regards to "no effect" – it has been reported as not significantly different with both 1st order and 2nd order tests and possible reasons given throughout the thesis. However, a power analysis will be considered for publications.

It would help to have the discussion restructured into subheadings.

** All experimental chapters are written in draft paper format for submission to journals which do not require subheadings. This is explained in the introduction.

Pg 52 (now pg 54). *There is mention of an analysis to compare core areas. I would like to see this.*

** A small sample does not allow for this.

Pg 56 (now pg 57). *Is the discussion about evolutionary traits of a species or the individual responses to environmental variation.*

** I have clarified this, but frequently, due to phylogenetic constraints, evolutionary and ecological effects are difficult to tease apart.

Pg 58 (now pg 59). *Numbered predictions would make them easier to follow.*

** Done

Pg 59 (now pg 60). *Same comments regarding MNA vs J-S.*

** See earlier comments regarding the necessity of using both J-S and MNA and why I used MNA based on the assumptions and predictions of the models.

Pg 60 (now pg 61). *All the analysis should be possible as a mixed model within the GLM framework. The response variables change but you could easily estimate differences between treatments. Grid should be a random effect.*

** A mixed model would be good, and I will consider it for publication. However, the results would be compromised due to a small sample size. For this reason, grids cannot be separated out either, although, as stated, statistical analysis did not show any significant differences between the grids.

Pg 62 (now pg 63). *Fig 5.2 would be better as a bar graph.*

** A line graph was used to show seasonal trends which is not clearly visible on a bar chart.

It would be easy to investigate the effect of season for recruitment and emigration with a GLM.

** It is clearly explained in the text why seasonal differences were not examined (small sample size; previous study with larger sample size found no differences)

Pg 64 . The interaction reported in the second paragraph makes the conclusion more complicated than reported in the text. Differences between males and females depend on grid type. The results need to specify this.

** Due to small sample sizes, grid could not be separated out as a random effect.

(pg 64) I'm unfamiliar with the term "range span"

** Clarified.

The last sentence in the results reports significant differences with no supporting statistics etc.

** The statistical analysis reported was a Tukey HSD post hoc test, as stated. This follows directly after a sentence describing the results from the corresponding GLM and the relevant figure.

The discussion could be divided into subheadings

** All experimental chapters are written in draft paper format for submission to journals which do not require subheadings. This is explained in the introduction.

Pg 66 (now pg 67). *"However, no differences in density…." This would be a good place to bring in Weins (1977) as no change in density is generally considered as strong evidence for lack of competition.*

** I have made an argument as to why no differences in densities can still indicate competition with references and examples from other small mammal studies.

Pg 73 (now pg 74). *Some detail is needed regarding "familiar" and "unfamiliar" indidividuals.*

** Behavioural studies frequently use the terms familiar (to indicate individuals that may have had contact with each other) and unfamiliar (individuals who in all probability have never come into contact with each other i.e. from different sites). These terms are defined in text.

Pg 74 (now pg 75). *I was confused by the terms here – "avoidance", "passive avoidance", "Active avoidance" and "ignore" seem to be used interchangeably.*

** Behavioral categories are explicitly defined so as to avoid confusion between active avoidance, passive avoidance and ignore behaviours.

This experiment is a classic log-linear design but there are some issues regarding non-independence.

** The experiment does lend itself to log-linear analysis. However, because the data were normally distributed and a GLM sufficiently answers the questions asked, so a GLM was used.

Pg 81 (now pg 82). *One major conclusion is that there are high levels of diet overlap with which I disagree – figure 2.2 shows substantial differences. Even in the dry season, which is the most limiting time, diets seems to diverge. Thus some careful reconsideration is needed.*

** I agree with the examiner that diets seem to diverge. However, when invertebrates (which are the preferred food of sengi's) are freely available, *E. myurus* decreases their consumption of invertebrates. Why? At the same time, *M. namaquensis* appears to increase the use of this dietary item, while restricting *E. myurus* access to invertebrates. Figure 2.1 shows overall

dietary items which does seem to indicate a lack of overlap. However, both Figure 2.2 (which shows seasonal overlap) and the overlap equations (Pianka, 1973; which is the standard reference for small mammal studies, perhaps due to slight modifications in the assumptions) show a high amount of overlap.

Pg 84 (now pg 85). *How does* E. myurus *restrict the breeding season of* M. namaquensis*? This is not clear from the data presented, looking at Fig 5.2.*

** As stated in the introduction, in the present study, both species have restricted breeding seasons compared to elsewhere in their range. As *E. myurus* dominates the use of insects, an essential source of protein which is important for breeding, earlier than *M. namaquensis,* it is probable that *M. namaquensis* breeding is restricted.

Pg 87 (now pg 88). *There is mention of* E. myurus *dominating food resources over* M. namaquensis – *this looks like new information.*

** Although I cannot find what is being referred to, all the results have been discussed in the individual chapters – I am trying to tie together all the information and propose possible reasons for coexistence.

Also, were those 5 behaviours reported? It would be interesting to see how they compare.

** Again, I cannot seem to find this reference, but the behaviours discussed would be the same as those referred to in the behavioural chapter.



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12 October 2009

Prof. Neville Pillay (supervisor)
12 October 2009