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Capture from the wild has long-term costs on reproductive success in Asian elephants

Mirkka Lahdenperä, John Jackson, Win Htut and Virpi Lummaa

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Review timeline

Original submission:	4 July 2019
1st revised submission:	5 September 2019
2nd revised submission:	16 September 2019
Final acceptance:	17 September 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2019-1584.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
N/A

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
In this paper, the authors report analysis of a long-term dataset of working elephants in Myanmar. The authors compare the reproductive outputs of wild-caught and captive-born individuals, which are housed and worked under similar conditions. Results showed that wild-caught females had substantially poorer reproductive outcomes over their lifetimes, which is interpreted as a possible consequence of the stress of capture and training. The consequences of these patterns are discussed in reference to the impacts of captive breeding on wild-caught animals, particularly for the long-term sustainability of captive programs.

I enjoyed reading this paper, which was well written. The dataset is outstanding for a study of this type, and the analysis is appropriate to the questions asked. The results have implications for captive programs of long-lived species, including the sourcing of animals, welfare, and population management.

Overall I found the analysis and its interpretation compelling and professionally presented. I have no further comments.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
Overarching comments:
1. This research interrogates studbook data for Asian elephants held in timber camps in Myanmar between 1942 and 2011. Females born in timber camps, that had not lived in the wild or been subject to capture, are compared with females captured from the wild to be used in the same timber camps. Compared to captive-born females, wild-caught females are found: to be less likely to produce at least one calf in their lifetime; to produce fewer calves, both over their lifetime and at peak reproductive ages; and to begin breeding at an older age. Calves from wild-caught mothers are also found to be more likely to die before the age of five years than calves from captive-born mothers.
2. This is a well written and thorough research paper, on a topic that has wide applicability and interest and which fulfils the criteria for publication in this journal. Elephants continue to be captured from the wild to bolster captive populations that are unsustainable. This research therefore has important implications for elephants, as well as other species subject to wild capture for various reasons, as stated by the authors.
3. The MTE database has been used as the basis for numerous publications, but I believe this is original research that has not been published elsewhere. Jackson et al (2019) report patterns of age-specific reproduction from the same elephant population and compare data for captive-born and wild-caught females, but this is developed and explored in detail in this paper. That said, it would be beneficial to highlight the link to this paper more clearly in the Introduction.
4. Whilst not explicitly stated by the authors, elephants born in timber camps are used as the 'norm' against which the reproduction of wild-caught females is measured. Results are interpreted as showing the damaging effects of capture. The authors state that wild-caught females have a "reduction in their lifetime reproduction probability" (Line 253-4) and wild-caught females have "delayed onset of reproduction" (Line 219). Studies of elephants in other captive settings, namely zoos, have found captive-born elephants to begin breeding significantly

younger than counterparts in the wild (e.g. Clubb et al. 2009). Could some of the results therefore be explained by captive elephants having an artificially enhanced reproductive performance compared to elephants born in the wild, due to provisioning, health care and so on, rather than capture from the wild having an adverse effect? This could be the case for age at onset of reproduction. It would not explain why wild-caught elephants then outperform captive-borns later in life, unless captive-borns are not only dying younger but also suffer conditions that impair reproduction for some time prior to death (McCleery et al. 2008) and/or undergo early reproductive senescence (e.g. Clubb et al. 2009). The Authors do note in the Discussion that "some captive animals are healthier, live longer and have a higher reproductive success than their wild counterparts" (Lines 354-356) and this leads to questions about "whether captive populations can be used as reference groups for species-typical parameter values" (Lines 359-360). If indications are that captive-born elephants are therefore not necessarily the 'norm', interpretation of the results is likely to differ somewhat to that which is presented. It would benefit the paper in my opinion to therefore consider this alternative in the Discussion and to make the language more neutral in earlier sections, such that authors are testing for differences in the onset of reproduction etc. Reference to data from free-living wild Asian elephants, where this exists, would benefit this discussion. This, however, is a minor point that would not require major revision. Other minor points are noted below for attention.

Specific comments:

Introduction
Line 62: 'for illegal trade' should I think be be 'via illegal trade'

Lines 65-66: Abnormal deliveries and stillbirths in captive elephants are said to 'reflect the vast differences between zoos and the wild', citing Clubb & Mason 2002. This was the hypothesised cause of the results found in this report, but it was not explicitly tested. It would therefore be more accurate to say 'likely' or 'hypothesised'.

Line 87: authors state 'Importantly, we investigate whether the effect of wild-capture on reproduction...'. Reference to Jackson et al (2019) here would confirm to the reader that such differences have already been found, and would not give the impression that the authors are pre-empting their findings.

Line 97: It is not entirely clear what is meant by 'breeding rates are natural'. Is this in comparison to wild Asian elephants?

Methods
Line 151-152: In analyses of 'Lifetime Reproductive Probability', it is not clear whether stillborn calves were included or just liveborns.

Line 191: meaning of 'but no main effect' in brackets requires more explanation.

Lines 191 and 196: what is meant by 'vital rates'?

Line 198: the term 'reproductive success' is used which appears to be equivalent to age-specific reproduction. To avoid confusion, I suggest using the same terms throughout.

Line 219: the authors speak of wild-caught females having "delayed onset of reproduction" whereas studies have found that captive-born elephants begin breeding early when compared to free-living elephants in the wild (e.g. Clubb et al. 2009). See overarching comments above.

Line 246: “maternal age and presence” is controlled for in the model. A little more explanation as to what is meant by ‘presence’ would help interpretation.

Line 265: the term “breeding in a given year” could cause confusion given that different cohorts are investigated. “Breeding at a given age” would be clearer.

Supplementary Material Line 12: Reasoning for grouping data for different camps based on proximity, elevation and sample size requires further explanation. What hypotheses are being tested? Have previous studies found similarities in measures based on this categorisation?

Supplementary Material Lines 23-25: Were censored calves excluded from analyses, i.e. those that had not yet reached five years of age? Methods do not include the year range for calf data.

Results
Line 295: A sentence or two on what is meant by “selective disappearance” would help the reader follow the reasoning more effectively.

Figure S2: Further explanation is needed in the Figure caption of the categories of “Age at capture”, similar to the caption for Figure 2.

Figure 2b): This is a complex graph to interpret. It is used to illustrate the finding that wild-caught females caught at older ages have a greater reduction in reproductive rates immediately after capture than those caught at a younger age. Some additional labels or circles to highlight the mean annual birth rate immediately after capture for each age group would draw the eye to the key parts of the graph.

Figure 5 and Figure S5: Sample size given (2471 calves and 1033 mothers) differs to the sample size provided in the text (2423 calves and 1030 mothers) (Lines 20-21 in Supplementary material).

Figure S3: Colour gradients used to denote different birth cohorts are quite difficult to differentiate. Different symbols, in addition to the different colours, would make this easier.

Discussion
Line 349: A more recent reference that the 2002 reference used is needed to support the statement that “60-80% of the current captive elephants in zoos are wild-caught”.

Line 387: A little further explanation is needed in the text as to what is meant by “selective (dis)appearance” to help contextualise the discussion that follows.

Line 414: The potential evolutionary consequences of wild-capture on elephant populations is a very interesting proposal. A couple more sentences to expand on this idea would really add to the paper.

Decision letter (RSPB-2019-1584.R0)

01-Aug-2019

Dear Dr Lahdenperä:

Your manuscript has now been peer reviewed and the reviews have been assessed by an

Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, there is general agreement that this is a very interesting manuscript and data-set, but the reviewers have raised some issues, and I also have some points that I believe need to be addressed. We would like to invite you to revise your manuscript to address these concerns.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Professor Loeske Kruuk
Editor
mailto: proceedingsb@royalsociety.org

Editor comments (Loeske Kruuk)
I appreciate that you are showing differences between wild-caught vs captive individuals, but as the paper stands I am not entirely convinced by the theme of 'negative effects of capture'. Could there not be an equally (or potentially more) plausible explanation that conditions are better for elephants in captivity, so they have higher reproductive rates - lifelong effects of conditions during juvenile development are well established in mammals. By the same scenario, it could presumably just be that the longer an elephant has been in captivity, the better condition it is in, and the higher its performance - this would fit with what you show in Figure 3. Ref 2 is saying something very similar in their point 4: i'e. it's not necessarily damaging effects of capture. So it seems like there is an alternative explanation of potentially long-lasting, potentially intergenerational beneficial effects of being looked after better in captivity, which needs to be acknowledged. As a starting point, what if captive-born animals are simply larger because they or their mothers have had more food, and this has the usual beneficial effect of larger size being associated with higher reproductive success?

The obvious test of this scenario would be to see what captivity did to body condition, and then

whether there were still differences in reproductive success if individual condition was also in the model. You mention that body condition is assessed monthly, so I assume you have data on it. Please can you therefore check whether there are differences in body size and body condition between wild-caught versus captive elephants, and whether any such differences are relevant to the differences in reproduction? The Introduction and Discussion will then need some rewording to acknowledge the different possible explanations.

Associate Editor
Board Member: 1
Comments to Author:
RSPB-2019-1584 uses an impressively large longitudinal and cross-generational data set from captive Asian elephants working in the timber industry in Myanmar to compare survivorship and reproductive success in wild captured vs. captive-born individuals. Their results clearly demonstrate capture effects - mostly negative - that decrease reproduction and reproductive success in wild-captured animals relative to captive-born counterparts. They are also able to use analyses that take time since capture into account to argue that capture stresses experienced by wild-caught animals are likely to drive many of these outcomes. These results are important with specific regard to elephant conservation and should raise questions and concerns as well as fuel future study of the immediate and evolutionary consequences of capture for other animal species. These data also demonstrate that captive individuals might not be appropriate to use as reference populations for estimating species-specific trait values.
This is a well written and clear paper with obvious potential applicability to basic and applied questions in life-history evolution and conservation. I did not see any major concerns. Neither did the reviewers, who both viewed the paper as a whole very positively. Reviewer 2 did bring up some minor points that do need to be addressed, including but not limited to a potential alternative interpretation of one result.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
In this paper, the authors report analysis of a long-term dataset of working elephants in Myanmar. The authors compare the reproductive outputs of wild-caught and captive-born individuals, which are housed and worked under similar conditions. Results showed that wild-caught females had substantially poorer reproductive outcomes over their lifetimes, which is interpreted as a possible consequence of the stress of capture and training. The consequences of these patterns are discussed in reference to the impacts of captive breeding on wild-caught animals, particularly for the long-term sustainability of captive programs.

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Overall I found the analysis and its interpretation compelling and professionally presented. I have no further comments.

Referee: 2

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Figure S3: Colour gradients used to denote different birth cohorts are quite difficult to differentiate. Different symbols, in addition to the different colours, would make this easier.

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Line 387: A little further explanation is needed in the text as to what is meant by "selective (dis)appearance" to help contextualise the discussion that follows.

Line 414: The potential evolutionary consequences of wild-capture on elephant populations is a very interesting proposal. A couple more sentences to expand on this idea would really add to the paper.

Author's Response to Decision Letter for (RSPB-2019-1584.R0)

See Appendix A.

Decision letter (RSPB-2019-1584.R1)

11-Sep-2019

Dear Dr Lahdenperä

I am pleased to inform you that your manuscript RSPB-2019-1584.R1 entitled "Capture from the wild has long-term costs on reproductive success in Asian elephants" has been accepted for publication in Proceedings B.

Thank you for the very thorough (and interesting!) responses to the previous reviewer and editorial comments (and especially for clarifying the distinction between timber vs zoo elephants). The Associate Editor has recommended one minor revision to your manuscript. Therefore, please could you make this change, and check over and then submit a final version? Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link

http://datadryad.org/submit?journalID=RSPB&manu=(Document not available) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Yours sincerely,

Professor Loeske Kruuk
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor:
Comments to Author:
The authors have done an excellent job of responding to the criticisms and suggestions from the editors and reviewers, including what I view as a thoughtful and satisfactory response to the point that Reviewer 2 raised regarding an alternative explanation for the results. I just have one additional request: a citation is needed for the assertion on line 134 that the training process for captive-born elephants is "considerably less stressful".

Author's Response to Decision Letter for (RSPB-2019-1584.R1)

See Appendix B.

Decision letter (RSPB-2019-1584.R2)

17-Sep-2019

Dear Dr Lahdenperä

I am pleased to inform you that your manuscript entitled "Capture from the wild has long-term costs on reproductive success in Asian elephants" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

Your article has been estimated as being 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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An e-mail request for payment of any related charges will be sent out shortly. The preferred payment method is by credit card; however, other payment options are available.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Dear Prof. Loeske Kruuk,

We thank you for the opportunity to revise our manuscript entitled "Capture from the wild has long-term costs on reproductive success in Asian elephants" that we recently submitted to *Proceedings of the Royal Society B*. We have now addressed all the comments made by the editors and both referees, and we feel that the clarity and quality of our message has been greatly enhanced as a direct result of all these constructive comments. Below is a detailed description on how each comment has been dealt with (line numbers refer to the clean version of the ms without track changes). The comments by the editors and both referees are in italics, while ours follow in bold. After our responses we have included the 'tracked changes' version of the ms.

Yours sincerely,

Mirkka Lahdenperä
John Jackson
Win Htut
Virpi Lummaa

COMMENTS BY THE EDITOR (Loeske Kruuk)

I appreciate that you are showing differences between wild-caught vs captive individuals, but as the paper stands I am not entirely convinced by the theme of 'negative effects of capture'. Could there not be an equally (or potentially more) plausible explanation that conditions are better for elephants in captivity, so they have higher reproductive rates - lifelong effects of conditions during juvenile development are well established in mammals. By the same scenario, it could presumably just be that the longer an elephant has been in captivity, the better condition it is in, and the higher its performance - this would fit with what you show in Figure 3. Ref 2 is saying something very similar in their point 4: i'e. it's not necessarily damaging effects of capture. So it seems like there is an alternative explanation of potentially long-lasting, potentially intergenerational beneficial effects of being looked after better in captivity, which needs to be acknowledged. As a starting point, what if captive-born animals are simply larger because they or their mothers have had more food, and this has the usual beneficial effect of larger size being associated with higher reproductive success?

The obvious test of this scenario would be to see what captivity did to body condition, and then whether there were still differences in reproductive success if individual condition was also in the model. You mention that body condition is assessed monthly, so I assume you have data on it. Please can you therefore check whether there are differences in body size and body condition between wild-caught versus captive elephants, and whether any such differences are relevant to the differences in reproduction? The Introduction and Discussion will then need some rewording to acknowledge the different possible explanations.

We thank you for bringing up this plausible alternative explanation. Although the alternative explanation is possible and we have now added it to the Introduction and Discussion (see lines 47-49 and 349-358) and in our response to reviewer 2, there are

several reasons why we think our results are due to negative effects of capture and not due to positive effects of being looked after in captivity.

First, wild-born elephants also have a substantially increased mortality following capture, which is greatest during the year of capture, but lasts for approximately 10 years (*Lahdenperä et al. (2018) Differences in age-specific mortality between wild-caught and captive-born Asian elephants. Nature Communications*). It is hard to see why the effects of capture on reproduction and mortality would persist for a decade if they were driven by better nutrition for elephants in captivity. We expect that the catch-up in body condition of wild-caught animals would be quicker if better care was the cause of the differences we observe. This negative effect of capture on mortality is also greater in elephants captured at older ages, in line with the current study. The increased immediate mortality is likely to be associated with capture-related injuries and trauma; mortality during the capture process is very high, estimated to be between 5-30% depending on the method (*Lair (1997) Gone Astray: The Care and Management of the Asian Elephant in Domesticity. FAO, Bangkok*; *Aung (1997) On the distribution, status and conservation of wild elephants in Myanmar. Gajah*). The subsequent taming and breaking also increases stress for the elephants (*Min-Oo (2010) The training methods used in Myanmar timber enterprise. Gajah).* Capture methods also selectively target young, apparently healthy individuals, yet despite such bias, survival and reproduction are lower than in similar-aged captive-born females. This adds to our conclusion that capture itself has negative effects on the demography of this population.

Second, concerning controlling for body condition in our analyses. Unfortunately we do not have historical data on body condition for the majority of the individuals used for our analyses (of which many are deceased), in order to re-run our statistical analyses whilst correcting for body weight. We only have access to frequent measures of body weight after 2012 for animals alive today, and only for a smaller subset of the population from camps in the Sagaing regional division. We apologise for the lack of clarity on this point, and we have now amended the ms to remove reference to the body weight data since it is largely irrelevant for the long-term data analysed in the current ms. However, to answer the point raised, a previous study that assessed the relationship between body size and reproduction in this subset of the population, which controlled for birth origin, did not find a statistically significant difference in the body size of wild-caught and captive-born females at reproductive ages (*Crawley et al. (2017) Is bigger better? The relationship between size and reproduction in female Asian elephants. Journal of Evolutionary Biology*). Additionally, there were no significant differences between wild-caught and captive-born individuals in male and female growth curves (*Mumby et al. (2015) Distinguishing between determinate and indeterminate growth in a long-lived mammal. BMC Evolutionary Biology*). Thus, while we could not assess differences in body condition between captive-born and wild-caught females included in this study, previous studies have not found evidence for differences. We now point this out on lines 105 and 353-354.

Third, timber elephants are not comparable to zoo elephants or many other captive animals because they receive only minimal supplementation (occasional seasonal fruit and rice when travelling) and instead forage naturally outside of working hours in the nearby forests. We have now added a sentence about the low provisioning in this population to the ms, see lines 99-100. Because timber elephants work during the day, they have significantly less opportunities to forage during this time compared to wild

elephants. Therefore, timber elephants do not receive foraging benefits from their captive environment.

Fourth, and perhaps the most compelling argument against the care of the timber elephants leading to better reproduction in captive-born elephants is a comparison with zoo and wild elephants. Zoo elephants receive up to date veterinary care and food/other resources, yet have reduced survival and reproduction compared to timber elephants. (*Clubb et al. (2008) Compromised survivorship in zoo elephants. Science*; *Clubb & Mason (2002) A Review of the Welfare of Zoo Elephants in Europe).* The negative effects in zoos have been observed despite the fact that zoo elephant calves have been found to be heavier than calves in timber camps (*Clubb et al. (2009) Fecundity and population viability in female zoo elephants: problems and possible solutions. Animal Welfare*) and there have also been suggestions that adult elephants in zoos are overweight, potentially explaining issues with reproduction. Importantly, timber elephants have demographic rates that are more similar to (but not higher than) wild populations (*de Silva et al. (2013) Demographic Variables for Wild Asian Elephants Using Longitudinal Observations. PLoS ONE*). Although studies on wild Asian elephants are limited, the mortality rates in captive-born elephants resemble wild African elephant mortality rates (*Clubb et al. (2008) Science*). Fecundity is also not increased in captive-born females in the current study; one study on wild Asian elephants found that the average fecundity for breeding females was 0.157, compared to 0.074 in captive-born females in our study (*de Silva et al. (2013) PLoS ONE*). We now point these comparisons out in the ms on lines 68-69, 354-355.

All of these points suggest that the findings reported in our study are due to negative capture and taming effects, not due to the beneficial effects of the captive environment on captive-born animals. We hope that you agree.

COMMENTS BY THE ASSOCIATE EDITOR

RSPB-2019-1584 uses an impressively large longitudinal and cross-generational data set from captive Asian elephants working in the timber industry in Myanmar to compare survivorship and reproductive success in wild captured vs. captive-born individuals. Their results clearly demonstrate capture effects - mostly negative - that decrease reproduction and reproductive success in wild-captured animals relative to captive-born counterparts. They are also able to use analyses that take time since capture into account to argue that capture stresses experienced by wild-caught animals are likely to drive many of these outcomes. These results are important with specific regard to elephant conservation and should raise questions and concerns as well as fuel future study of the immediate and evolutionary consequences of capture for other animal species. These data also demonstrate that captive individuals might not be appropriate to use as reference populations for estimating species-specific trait values. This is a well written and clear paper with obvious potential applicability to basic and applied questions in life-history evolution and conservation. I did not see any major concerns. Neither did the reviewers, who both viewed the paper as a whole very positively. Reviewer 2 did bring up some minor points that do need to be addressed, including but not limited to a potential alternative interpretation of one result.

Thank you for these positive comments. We have now added the alternative interpretation suggested by the Referee 2 and Editor to the Introduction and Discussion (lines 47-49 and 349-358). We hope that overall, all modifications has improved the manuscript further.

COMMENTS BY REFEREE 1

In this paper, the authors report analysis of a long-term dataset of working elephants in Myanmar. The authors compare the reproductive outputs of wild-caught and captive-born individuals, which are housed and worked under similar conditions. Results showed that wild-caught females had substantially poorer reproductive outcomes over their lifetimes, which is interpreted as a possible consequence of the stress of capture and training. The consequences of these patterns are discussed in reference to the impacts of captive breeding on wild-caught animals, particularly for the long-term sustainability of captive programs.

I enjoyed reading this paper, which was well written. The dataset is outstanding for a study of this type, and the analysis is appropriate to the questions asked. The results have implications for captive programs of long-lived species, including the sourcing of animals, welfare, and population management.

Overall I found the analysis and its interpretation compelling and professionally presented. I have no further comments.

Thank you, we are happy to hear the Referee found our manuscript important, professional and fluent and hope that our newest changes have improved the text and clarity further.

COMMENTS BY REFEREE 2

Overarching comments:
1. This research interrogates studbook data for Asian elephants held in timber camps in Myanmar between 1942 and 2011. Females born in timber camps, that had not lived in the wild or been subject to capture, are compared with females captured from the wild to be used in the same timber camps. Compared to captive-born females, wild-caught females are found: to be less likely to produce at least one calf in their lifetime; to produce fewer calves, both over their lifetime and at peak reproductive ages; and to begin breeding at an older age. Calves from wild-caught mothers are also found to be more likely to die before the age of five years than calves from captive-born mothers.
2. This is a well written and thorough research paper, on a topic that has wide applicability and interest and which fulfils the criteria for publication in this journal. Elephants continue to be captured from the wild to bolster captive populations that are unsustainable. This research therefore has important implications for elephants, as well as other species subject to wild capture for various reasons, as stated by the authors.
3. The MTE database has been used as the basis for numerous publications, but I believe this is original research that has not been published elsewhere. Jackson et al (2019) report patterns of age-specific reproduction from the same elephant population and compare data for captive-born and wild-caught females, but this is developed and explored in detail in this paper. That said, it would be beneficial to highlight the link to this paper more clearly in the Introduction.

Thank you, and we are glad to hear that the Referee 2 found our research paper important especially for elephant welfare and also potentially for other animals being captured from the wild. We have now added a sentence to the Introduction explaining the link to the paper by Jackson et al. 2019 (see lines 88-91).

4. Whilst not explicitly stated by the authors, elephants born in timber camps are used as the 'norm' against which the reproduction of wild-caught females is measured. Results are interpreted as showing the damaging effects of capture. The authors state that wild-caught females have a "reduction in their lifetime reproduction probability" (Line 253-4) and wild-caught females have "delayed onset of reproduction" (Line 219). Studies of elephants in other captive settings, namely zoos, have found captive-born elephants to begin breeding significantly younger than counterparts in the wild (e.g. Clubb et al. 2009). Could some of the results therefore be explained by captive elephants having an artificially enhanced reproductive performance compared to elephants born in the wild, due to provisioning, health care and so on, rather than capture from the wild having an adverse effect? This could be the case for age at onset of reproduction. It would not explain why wild-caught elephants then outperform captive-borns later in life, unless captive-borns are not only dying younger but also suffer conditions that impair reproduction for some time prior to death (McCleery et al. 2008) and/or undergo early reproductive senescence (e.g. Clubb et al. 2009). The Authors do note in the Discussion that "some captive animals are healthier, live longer and have a higher reproductive success than their wild counterparts" (Lines 354-356) and this leads to questions about "whether captive populations can be used as reference groups for species-typical parameter values" (Lines 359-360). If indications are that captive-born elephants are therefore not necessarily the 'norm', interpretation of the results is likely to differ somewhat to that which is presented. It would benefit the paper in my opinion to therefore consider this alternative in the Discussion and to make the language more neutral in earlier sections, such that authors are testing for differences in the onset of reproduction etc. Reference to data from free-living wild Asian elephants, where this exists, would benefit this discussion. This, however, is a minor point that would not require major revision. Other minor points are noted below for attention.

Thank you for highlighting this important point, which made us think carefully about the findings of our ms, especially the age at first reproduction result. One sentence that may have lead Referee 2 to think that the captive-born animals wouldn't be the "norm" (*"some captive animals are healthier, live longer and have a higher reproductive success than their wild counterparts"*) was confusing and we have changed it now to (lines 365-367: *"Although some species in captivity are healthier, live longer and have a higher reproductive success than their wild counterparts, other species perform less well in captivity")* as we refer to other animal species that seem to cope well in captive conditions, e.g. zoos.

There are however several reasons why we do not think that the captive-born elephants in this population have artificially enhanced reproduction like zoo elephants due to provisioning (which is minimal, see lines 99-100), compared to wild elephants (also see our response to Editor Loeske Kruuk's comment on the same issue). In addition to the comments made in our previous response, we found that the onset of reproduction in captive-born elephants occurred between 12-13 (see ms, lines 220-221, 267-269), which is comparable to other wild populations, for example in Sri Lanka *(de Silva (2013)*), whereas zoo elephants have been estimated to have 3-5 years earlier age at first reproduction (*Clubb & Mason (2002)*). In our population it is rare to give birth before age 13 (only 3% of captive-born females, lines 221-223). In the analysis of age at first reproduction we also only included females captured before, or giving birth after (captive-born) age 13, and so the results would not be confounded by later entry to the population for wild-born animals or early reproduction for captive-born animals (see lines 219-223). Nevertheless, we found that the age at first reproduction for captive-born females was 2 years earlier

than for wild-caught females, suggesting that this truly is the effect of postponing the first reproduction for those being captured from wild.

Furthermore, as the Referee says, this alternative explanation of enhanced reproduction would not explain why wild-caught elephants then outperform captive-born females later in life unless captive-born elephants died at younger ages or suffered from impaired reproduction at old age. This is not the case here because capture reduces the median lifespan of wild-caught elephants of both sexes by several years compared to captive-born elephants (*Lahdenperä et al. 2018*). Unfortunately it is difficult to say whether captive-born elephants would suffer from some reproductive complications at older ages leading to reproductive cessation. We do not have that kind of physiological data at the moment on the elephants. However, the stillbirth probability (as well as calf mortality generally) for captive-born females is much lower than in zoo elephants (only 4% (*Mar et al. (2012) Causes and correlates of calf mortality in captive Asian elephants (Elephas maximus) PlosOne*) suggesting that captive-born timber elephants may not have the reproduction issues that are found in zoos. We also controlled for individual lifespan in age-specific reproduction analyses, which therefore should not confound our analyses.

We have now added this alternative explanation to Introduction and Discussion (see lines47-49 and 349-358). We have also tried to use more neutral language in testing differences between wild-caught and captive-born animals (see e.g. lines 218-219), and added references to wild Asian elephants (see line 355). We hope that the Referee is happy with these further changes.

Specific comments:

Introduction
Line 62: 'for illegal trade' should I think be be 'via illegal trade'

Corrected.

Lines 65-66: Abnormal deliveries and stillbirths in captive elephants are said to 'reflect the vast differences between zoos and the wild', citing Clubb & Mason 2002. This was the hypothesised cause of the results found in this report, but it was not explicitly tested. It would therefore be more accurate to say 'likely' or 'hypothesised'.

Thank you for the clarification, changed in line with the suggestion.

Line 87: authors state 'Importantly, we investigate whether the effect of wild-capture on reproduction...'. Reference to Jackson et al (2019) here would confirm to the reader that such differences have already been found, and would not give the impression that the authors are pre-empting their findings.

Thank you, we have now clarified the link to this reference, see lines 88-91.

Line 97: It is not entirely clear what is meant by 'breeding rates are natural'. Is this in comparison to wild Asian elephants?

We mean here that the breeding rates are natural in the sense that breeding rates are unmanaged by humans as elephants are not aided in mating or calving. We have now added clarification to the sentence, lines 102-104.

Methods
Line 151-152: In analyses of 'Lifetime Reproductive Probability', it is not clear whether stillborn calves were included or just liveborns.

All births were included in Lifetime Reproduction Probability analyses, which included those that were stillborn (line 147).

Line 191: meaning of 'but no main effect' in brackets requires more explanation.

We have now clarified this, see lines 181-187.

Lines 191 and 196: what is meant by 'vital rates'?

We have changed this to survival and reproduction (lines 189-190 and 194).

Line 198: the term 'reproductive success' is used which appears to be equivalent to age-specific reproduction. To avoid confusion, I suggest using the same terms throughout.

The referee is right, and we have changed this to avoid confusion. We have also changed all terms "reproductive success" either to age-specific reproduction or reproduction probability when we actually talk about age-specific reproduction.

Line 219: the authors speak of wild-caught females having "delayed onset of reproduction" whereas studies have found that captive-born elephants begin breeding early when compared to free-living elephants in the wild (e.g. Clubb et al. 2009). See overarching comments above.

Please see our response to the major comment above. The age at first reproduction of captive-born elephants in our population closely resembles estimates in wild populations.

Line 246: "maternal age and presence" is controlled for in the model. A little more explanation as to what is meant by 'presence' would help interpretation.

We apologise that these details were not in the manuscript or supplementary material. We have now added them to the supplementary file (due to length restrictions in the ms), see lines 37-43 from SI.

Line 265: the term "breeding in a given year" could cause confusion given that different cohorts are investigated. "Breeding at a given age" would be clearer.

Thank you, changed.

Supplementary Material Line 12: Reasoning for grouping data for different camps based on proximity, elevation and sample size requires further explanation. What hypotheses are being tested? Have previous studies found similarities in measures based on this categorisation?

We agree that our justification of controlling for spatial variation in reproduction was not clear, and have amended the supplementary material, lines 12-18, to make this clear. Accounting for spatial variation in this system is important because elephants live and work across Myanmar, and experience differences in forest cover, habitat availability and climate conditions. We grouped regional divisions together to capture elephants experiencing similar conditions, but also to make sample sizes between groups more comparable.

Supplementary Material Lines 23-25: Were censored calves excluded from analyses, i.e. those that had not yet reached five years of age? Methods do not include the year range for calf data.

Calves censored before the age of 5 were included in analysis, with their yearly survival coded as 'alive' (=1) until censoring (see lines 234-235 in the ms). The sentence in Supplementary material, lines 27-29, refers to excluding calves and mothers from the analysis that did not have exact or censored lifespan recorded at all (calves) or after the calf was born (mother). We have now modified the sentence to avoid confusion. We have also reported the year range and sample size of calf data in lines 229-231.

Results
Line 295: A sentence or two on what is meant by "selective disappearance" would help the reader follow the reasoning more effectively.

Thank you, we have now added clarification, see lines 294-296.

Figure S2: Further explanation is needed in the Figure caption of the categories of "Age at capture", similar to the caption for Figure 2.

We have now amended the captions for figure S2 and Figure 2 to make this clearer.

Figure 2b): This is a complex graph to interpret. It is used to illustrate the finding that wild-caught females caught at older ages have a greater reduction in reproductive rates immediately after capture than those caught at a younger age. Some additional labels or circles to highlight the mean annual birth rate immediately after capture for each age group would draw the eye to the key parts of the graph.

We apologise that this was confusing, and we have now clarified the sentence in the Results section (see lines 307-312), saying that there are differences in the reproductive rate between females captured at different ages (visible from Figure 2b) and that the effects of capture were more detrimental for females captured at older ages (visible from Figure S2). The finding of a larger decrease immediately after capture for females caught at older ages isn't visible clearly from Figure 2 because it doesn't directly compare reproduction probabilities between captive-born and wild-caught females (odds ratios are more illuminating here). We have also clarified the interpretation of these results/figures in the legends of Figure 2 and S2.

Figure 5 and Figure S5: Sample size given (2471 calves and 1033 mothers) differs to the sample size provided in the text (2423 calves and 1030 mothers) (Lines 20-21 in Supplementary material).

Thank you very much for spotting this error, the numbers were correct in the text. We have now corrected the numbers to figure legends.

Figure S3: Colour gradients used to denote different birth cohorts are quite difficult to differentiate. Different symbols, in addition to the different colours, would make this easier.

We have now used a facetted plot to distinguish between birth cohorts (relative to raw mean values), and hope that this is clearer.

Discussion
Line 349: A more recent reference that the 2002 reference used is needed to support the statement that "60-80% of the current captive elephants in zoos are wild-caught".

Thank you, we have now added a more recent reference to Prado-Oviedo et al. 2016 PLoSONE (for North American zoos) in addition to the Clubb and Mason 2002 reference (for zoos in Europe)(line 361).

Line 387: A little further explanation is needed in the text as to what is meant by "selective (dis)appearance" to help contextualise the discussion that follows.

We explain the meaning in the subsequent lines 397-407. We have also added a short explanation to lines 295-296.

Line 414: The potential evolutionary consequences of wild-capture on elephant populations is a very interesting proposal. A couple more sentences to expand on this idea would really add to the paper.

We thank the reviewer for this comment and agree that the long-term evolutionary consequences of human activity on wildlife populations is an interesting topic, which deserves further attention in future studies. We have now added a few more sentences and created an additional paragraph in the discussion (lines 409-421) in order to explore these ideas a little bit more.

Appendix B

Dear Prof. Loeske Kruuk,

We are happy to hear our manuscript RSPB-2019-1584.R1 entitled "Capture from the wild has long-term costs on reproductive success in Asian elephants" has been accepted for publication in Proceedings B. Below we reply to the remaining comment by the Associate Editor.

Yours sincerely,

Mirkka Lahdenperä on the behalf of all co-authors

Associate Editor:

Comments to Author:

The authors have done an excellent job of responding to the criticisms and suggestions from the editors and reviewers, including what I view as a thoughtful and satisfactory response to the point that Reviewer 2 raised regarding an alternative explanation for the results. I just have one additional request: a citation is needed for the assertion on line 134 that the training process for captive-born elephants is "considerably less stressful".

We are glad to hear the Associate Editor thinks our responses and modifications to the ms were satisfactory and thoughtful. We have now cited Lair 1997 and Zaw 1997 in row 134. The sentence says now “Captive-born elephants are also tamed around the age of 4-5 (Min-Oo 2010), but their training is thought to be easier and less stressful (Lair 1997, Zaw 1997)”.