Peer Community In Ecology

On the road to adulthood: exploring progressive changes in foraging behaviour during post-fledging immaturity using remote tracking

Blandine Doligez *based on peer reviews by* ***Juliet Lamb*** *and 1 anonymous reviewer*

Karine Delord, Henri Weimerskirch, Christophe Barbraud (2023) The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird. bioRxiv, ver. 6, peer-reviewed and recommended by Peer Community in Ecology.
https://doi.org/10.1101/2021.10.23.465439

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In most vertebrate species, the period of life spanning from departure from the growing site until reaching a more advanced life stage (immature or adult) is critical. During this period, juveniles are often highly vulnerable because they have not reached the morphological, physiological and behavioural maturity levels of adults yet and are therefore at high risk of mortality, e.g. through starvation, depredation or competition (e.g. Marchetti & Price 1989, Wunderle 1991, Naef-Daenzer & Grüebler 2016). In line with this, juvenile survival is most often far lower than adult survival (e.g. Wooller et al. 1992). In species with parental care, juveniles have to acquire behavioural independence from their parents and possibly establish their own territory during this period of life. Very often, this is also the period that is least well-known in the life cycle (Cox et al. 2014, Naef-Daenzer & Grüebler 2016) because of reduced accessibility to individuals and/or adoption of low conspicuous behaviours. Therefore, our understanding of how juveniles acquire typical adult behaviours and how this progressively increases their survival prospects is still very limited (Naef-Daenzer & Grüebler 2016), and questions such as the length of this transition period or the cognitive (e.g. learning, memorization) mechanisms involved remain largely unresolved. This is particularly true regarding the acquisition of independent foraging behaviour (Marchetti & Price 1989).

Because direct observations of juvenile behaviours are usually very difficult except in specific situations or at the cost of an enormous effort, the use of remote tracking devices can be particularly appealing in this

context (e.g. Ponchon et al. 2013, Kays et al. 2015). Over the past decades, technical advances have allowed the monitoring of not only individuals' movements at both large and small spatial scales but also their activities and behaviours based on different parameters recording e.g. speed of movement or diving depth (Whitford & Klimley 2019). Device miniaturization has in particular allowed smaller species to be equipped and/or longer periods of time to be monitored (e.g. Naef-Daenzer et al. 2005). This has opened up whole fields of research, and has been particularly used on marine seabirds. In these species, individuals are most often inaccessible when at sea, representing most of the time outside (and even within) the breeding season, and the life cycle of these long-lived species can include an extended immature period (up to many years) during which most of them will remain unseen, until they come back as breeders or pre-breeders (e.g. Wooller et al. 1992, Oro & Martínez-Abraín 2009). Survival has been found to increase gradually with age in these species before reaching high values characteristic of the adult stage. However, the mechanisms underlying this increase are still to be deciphered.

The study by Delord et al. (2023) builds upon the hypothesis that juveniles gradually learn foraging techniques and movement strategies, improving their foraging efficiency, as previous data on flight parameters seemed to show in different long-lived bird species. Yet, these previous studies obtained data over a limited period of time, i.e. a few months at best. Whether these data could capture the whole dynamics of the progressive acquisition of foraging and movement skills can only be assessed by measuring behaviour over a longer time period and comparing it to similar data in adults, to account for seasonal variation in relation to both resource availability and energetic demands, e.g. due to molt.

The present study (Delord et al. 2023) addresses these questions by taking advantage of longer-lasting recordings of the location and activity of juvenile, immature and adult birds obtained simultaneously to investigate changes over time in juvenile behaviour and thereby provide hints about how young progressively acquire foraging skills. This study is performed on Amsterdam albatrosses, a highly endangered long-lived sea bird, with obvious conservation issues (Thiebot et al. 2015). The results show progressive changes in foraging effort over the first two months after departure from the birth colony, but large differences remain between life stages over a much longer time frame. They also reveal strong variations between sexes and over time in the year. Overall, this study, therefore, confirms the need for very long-term data to be collected in order to address the question of progressive behavioural maturation and associated survival consequences in such species with strongly deferred maturity. Ideally, the same individuals should be monitored over different life stages, from the juvenile period up to adulthood, but this would require further technical development to release the issue of powering duration limitation.

As reviewers emphasized in the first review round, one main challenge now remains to ascertain the outcome of the observed behavioural changes in foraging behaviour: we expect them to reflect improvement in foraging skills and thus performance of juveniles over time, but this would need to be tested. Collecting data on foraging efficiency is yet another challenge, that future technical developments may also help overcome. Importantly also, data were available only for individuals that could be caught again because the tracking device had to be retrieved from the bird. Here, a substantial fraction of the loggers (one-fifth) could not be found again (Delord et al. 2023). To what extent the birds for which no data could be obtained are a random sample of the equipped birds would also need to be assessed. The further development of remote tracking techniques allowing data to be downloaded from a long distance should help further exploration of behavioural ontogeny of juveniles while maturing and its survival consequences. Because the maturation process explored here is likely to show very different characteristics (e.g. timing and speed) in smaller / shorter-lived species (see Cox et al. 2014, Naef-Daenzer & Grüebler 2016), the development of miniaturization is also expected to allow further investigation of post-fledging behavioural maturation in a wider range of bird species. Our understanding of this crucial life phase in different types of species should thus continue to progress in the coming years.

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Wunderle J. M. 1991. Age-specific foraging proficiency in birds. Current Ornithology, 8: 273-324.

Reviews

Evaluation round #4

DOI or URL of the preprint: https://doi.org/10.1101/2021.10.23.465439
Version of the preprint: 5

Authors' reply, 04 October 2023

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Decision by **Blandine Doligez**, posted 02 October 2023, validated 02 October 2023

Very minor revision

Dear authors,

Thank you for carefully editing the last version with the corrections suggested. I have still spotted a few additional ones that would need to be dealt with before final recommendation is made (as no further changes can be done later on). This should however be done very quickly... Sorry for the additional delay but this time it should be the last!

Here are the edits needed:

l. 114-119: the separators need adjustment: the sentence should read as:
*These included temporal (i.e. related to the month of the year) changes in activity parameters for all life-stages due **(i) to** environmental changes occurring throughout the seasons, **(ii) to** partial moulting which is suspected to occur outside the breeding period and to result in reduced activity for adults and immatures (i.e. more time 115 spent on the water; Weimerskirch et al. 2015, 2020), or **(iii) to** sex differences in flight performances (Shaffer 116 et al. 2001; Riotte-Lambert and Weimerskirch 2013; Clay et al. 2020).*

There are still a number of places where the double parentheses should be removed when a reference appears in a section that is already in parentheses (e.g. l. 66, l. 219). In these cases, the parentheses around the reference should be dropped. In the same way, l. 879, parentheses for the Smith reference should be around the year only.

Regarding the use of AICc: thanks for checking that results were unchanged with AICc instead of AIC. Thus I think there is no need to replace AIC by AICc in the ms. However, because readers may ask themselves the same question, I would simply add a short sentence to mention this clearly: "Using AICc to account for small sample sizes did not change model selection" (or something similar, when you mention AIC in methods, l. 238).

l. 834: there is no Table S6 (?)
l. 252: I would delete the second "inter-individual variability"
l. 258: I would delete the second "variability"
l. 438: seems like permit number has been forgotten, but I am not sure whether this is compulsory (would be better to mention them I think).
l. 348: add a "." after "sea"
l. 360: remove the "," after "albatrosses"
l. 428: add a "," before "which", and "which would still need" instead of "which still would need"
l. 490: remove the very first parenthesis (before i.e.)
l. 491; replace "of" by "in"

Evaluation round #3

DOI or URL of the preprint: https://doi.org/10.1101/2021.10.23.465439
Version of the preprint: 4

Authors' reply, 20 September 2023

Thank you for giving us the opportunity to revise our submitted manuscript.

Many thanks for the comments received, we believe they clearly improved the readability of the manuscript.

Please find in the attached documents detailed 1) responses to the reviewers comments (point-by-point responses) and 2) revised version with track changes.

Download author's reply

Decision by Blandine Doligez, posted 22 August 2023, validated 28 August 2023

A final minor revision (mostly text edits)

My deepest apologies again for the long delay in sending this decision. I thank the authors for their nice work on this new revised version. I feel that the concerns of the reviewers and myself have been nicely addressed and the manuscript is now much clearer and focused, and far better structured around the main question. I will be happy to recommend it for publication, after a series of points that I detail below have been corrected. Most of them deal with text edits / improvements (please read again the whole text carefully as I may have missed some mistakes), but there are a couple of more conceptual points, in particular the use of AICc, the differences between fig. 2 and 3, and adding a few more thoughts about the consequences of the results described for understanding the life-history of the species.

- l. 25: replace since by after ?
- l. 64: add a coma after "years" and change the parentheses for the reference
- table 2: although useful as noted by previous reviews, could be simplified to avoid repetitions for the three different parameters (basically nothing changes but the name of the parameter and direction of expected change). I believe that this table could be drastically reduced
- table 2 (and/or corresponding text): state clearly that the two hypotheses are not mutually exclusive?
- l. 111-116: add (i), (ii) and (iii) before to environmental..., to partial molting... and to sex differences... to clarify the structure of the sentence and ease the reading.
- l. 143: what former strategy? I do not understand here; the sentence may need to be clarified here
- l. 162: replace "regarding" by "with respect to"? Maybe "year" is also not the right term here since it does not refer to specific years but ages
- l. 167-168: "data on the three stages over a long period of time"
- l. 175: so the number of 10 min blocks was divided by 6 to compute a time in hours then?
- l. 206: "describe behaviours using gradients of activity" is not so clear to me. Do you simply mean here "changes in behaviour over time and stages"?
- l. 206 and 208 (and thereafter): not sure the acronyms PCS and PCJ are useful here (you anyway repeat what they correspond each time after, so I would simply remove them). You can then replace PC1S, PC2S etc. by their names directly.
- l. 215: double parenthesis
- l. 222: I would add here that interactions between stage and time were included as fixed effects to test for the prediction that differences should vanish with time passed since fledging.
- l. 231: have you checked whether using AIC corrected for small sample size (AICc) changed anything? If not, I would do it to test for the robustness of the results, as small samples are likely to lead to model overfitting (l. 469 and 477 indicate AICc, but the text mentions AIC?)
- l. 235-244: this section appears strange here, as it looks like a simple check of size dimorphism in this species, but with no apparent link to the main question of interest, here patterns of foraging activity. I would suggest deleting it completely except the sentence justifying what body size was not included as an explanatory variable (l. 241-244, adding the actual sample sizes) and move the analyses themselves (description and results l. 294-299, including table 7) as an appendix.

- l. 253 and 259: you can remove the second “inter-individual variability”
- l. 257: replace “found” by “retained”?
- l. 251-252: the interaction was clearly not supported for the second PCA axis for all stages (table 4 shows a difference of AIC of approx. 1000!) so something is wrong here: only the first axis is concerned and not the second? Please correct
- l. 270 (and 318): I do not think that the word “abrupt” is needed. It may look abrupt when the whole duration is considered, but may happen gradually during the first month (all being a question of time scale and reference). You can delete this and simply say “strong changes”. In the same vein, l. 320-321: you mention “also exhibited progressive change” and “gradual change” but this is quite opposite to abrupt. Please rewrite here for clarity.
- l. 306-308: I would place this sentence at the very beginning of this paragraph (general presentation of the study)
- l. 315: “the first months” (plural) – otherwise this is not coherent with the rest of the sentence
- l. 321: replace “and that” by “so that”. Yet, the previous sentences indicate that at least part of the activity parameters still differ between juveniles and other stages (proportion of time spent on water), so maybe be a bit more cautious here with respect to similarity?
- l. 326-328: not clear here: are the differences you refer to those observed during the first two months only? As said above, you also mention longer-term differences in this parameter. I think clarification is needed here.
- l. 328: a transition here before discussing the interpretation in terms of performance?
- l. 437: provide permit numbers here
- l. 480: parentheses to be displaced around references
- l. 336: is this really inconsistency? Is it not quite intuitive that immatures may behave “in between” juveniles and adults, and thus resemble the first in some aspects (or ins some periods) and the second in other aspects?
- l. 347: replace “of optimal behaviours” by “leading to sub-optimal behaviour”, and place it at the end of the sentence, since it is true for other mechanisms as well? (but be careful not to overinterpret results in terms of performance as noted by the first reviewer on the first version, and as mentioned here a few lines above).
- l. 344-350: I would place this paragraph before discussing the case of immatures (so before l. 333), as you mainly mention juveniles (see l. 349).
- l. 353-354: I do not understand this sentence: they behave differently than what: adults? other species? if adults, when? (since you mention that they readily use similar foraging strategies, so they do not behave differently then?). Please clarify here.
- l. 360-361: not sure that the shag example is a good one here, as it does not illustrate the idea of progressive improvement in flight performance, but compensation strategies for lower flight performance instead.
- l. 363: “fly over long distances away from”
- l. 365-367: I would simplify here by saying “The progressive change… could be either due to physical development or experience gain”.
- l. 368: “Elucidating the mechanisms of the transition…” would be more correct I think. Also add “however” to show that this remains a important question to tackle?
- l. 373: juvenile
- l. 378 (and 431): renewal or molt?
- l. 386: replace “this” by “the same” or “a similar”
- l. 388: male and female Amsterdam albatrosses
- l. 391-392: I’d suggest “Males in all stages did more bouts on water and juvenile males shorter wet bouts, compared to females”.

- l. 391-394: I would place the description of the differences observed between sexes before discussing its origin (thus before l. 388), and make only one single paragraph about sex differences.
- l. 396: double parentheses
- l. 402-404: this suggests strong selective pressures for decreasing size dimorphism. Are pressures that maintain this dimorphism known (e.g. sexual selection)? It could be worth saying a word about it here, as the paragraph ends a bit abruptly otherwise. Also, would a sentence like "Sex differences in the acquisition of foraging performance during the first months after fledging yet remain to be explored", to get back to the main question of the paper, namely ontogeny of this behaviour. Indeed, you did not test for a sex x phase x month elapsed since fledging interaction (but sample size does of not course not allow it here), which would be needed to test whether males and females acquire foraging skills with different speed (this could be expected if lighter females are more efficient?). Well, something like this to finish off this section would be good!
- l. 423-424: no need to repeat the stages here I think
- l. 427: replace "since" by "after"
- l. 427-428: is it possible to conclude from the results of the study that the lower survival observed for the first years in this species is unlikely to be fully explained by such an improvement in foraging ability, since parameters for juveniles reach the values observed for adults quite rapidly (even though some differences seem to remain longer)? I guess more detailed information would be needed to say so, especially data on the actual foraging performance realized (the amount or quality of preys obtained by juveniles), or at least on actual behaviour (the parameters used here remain rough when it comes to describe the behaviour itself). I think some kind of further thoughts on the results would be nice here to provide perspectives for future work or potential consequences for the understanding of the dynamics / evolution in this species... (and go beyond a simple summary of results!)
- l. 433: the "therefore" does not relate to the previous sentence (on sex differences). It would be better to rewrite here ("Overall", or "As a conclusion"?)
- l. 434: indicate that this still would need to be confirmed by directly assessing foraging performance (see above)?
- l. 491: quite difficult to read (three "of")... maybe consider rewriting? ("for all stages"?). Also, Figure 2 has three panels (a, b and c), which should be described in the legend.
- l. 492: double parenthesis to remove
- when comparing fig. 2a with 3a, and 2b with 3b, I do not understand why the pattern observed for the first 9 months in juveniles does not appear in the longer period. I acknowledge that the smoothing and other parameters of the models differ in both cases, but the decline (for the first PCA axis) and the increase (for the second axis) are not observed at all anymore (instead reverse tendencies appear!), which is confusing. This needs to be explained clearly.
- l. 512 and 516: I guess this is fig 3 not 2?

Evaluation round #2

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Version of the preprint: v1

Authors' reply, 05 June 2023

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Decision by **Blandine Doligez**, posted 11 December 2022, validated 12 December 2022

Revision needed

Dear authors,

My apologies for the delay in sending the decision about the revised version of your manuscript. Only one reviewer could assess this version and I also read it myself. Overall, the reviewer and I acknowledge the quality and quantity of work done on this revised manuscript, and I thank the authors for addressing with great care the concerns raised by reviewers on the first version, in particular with the new statistical approaches used (PCA and GAMM) and the caution when interpreting changes in foraging activity patterns.

As you will see, the reviewer still had a number of important remarks, mostly regarding the presentation of the study (presenting the objectives of the study, presenting the results and regarding figures and tables). I think that these suggestions would improve further the manuscript. Therefore, I encourage the authors to address them, and in particular:

- reduce the predictions at the end of the introduction to relate them to the first part of the section, i.e. focus on post-fledging learning while presenting more succinctly the need to account for other sources of changes in foraging behaviour (differences due to seasonal variations, molt or sex);
- reduce the description of the species movements in the methods to what is necessary here (maybe more as a discussion when comparing different life stages);
- present the results of PCA in a table to avoid redundancy since the exact same variables are retained for the axes in both cases;
- reorganise the result section so as to make the test of predictions more apparent; for each section, start with changes with time elapsed and differences between stages, which correspond to the main objectives here;
- reorganise tables and figures following the reviewer's suggestions to make them less numerous, clearer and more concise and avoid redundancy with the text.

In addition, I found the discussion quite long, and not so much focused on the central question of the acquisition of foraging skills in juveniles. While differences between sexes and in time are interesting, they could be reduced here (l. 997-1073).

Finally, I would like to raise one more important point: I am not so familiar with GAMMs, but in order to formally test whether juvenile gradually acquire foraging skills and whether their behaviour gradually becomes similar to that of adults, should an interaction between stage and time elapsed not be tested in the model? Indeed, juveniles are expected to differ from more experienced immatures / adults during a transitory learning phase and then no difference anymore is expected. This may be possible to model directly in GAMMs – again I am not familiar with these models, and I can see that different curves can be obtained by the smoothing procedure, which may be equivalent to a stage x time elapsed interaction. However, without clearly and directly testing such an interaction, how can we formally distinguish between year-round differences between stages (i.e. additive effects of stage and time elapsed) and gradual change in one stage only (i.e. an interaction between stage and time elapsed)? Random slopes test for individual variability in the change in activity with time elapsed, but this level of variability does not test for a global effect of stage that would structure such among-individual variability. I may have missed something there, but in this case I believe that this should be more clearly mentioned and explained. To illustrate this point (even though this is not so much related to changes in juveniles), when looking at figure S6: do immatures and adults differ in their activity pattern? The curves are slightly shifted in time, but because we have no idea of the variation around this smoothed curve, we cannot really assess from the figure whether the difference is statistically relevant or not. In other words, it seems clear that GAMMs allow different smoothers for different stages, but when can they be considered statistically different? (with comparison to differences between stages that would simply be additive to time elapsed). We miss information on variation around this smoothed curves and formal tests of different curves being statistically different.

Below a list of more detailed points that may need to be addressed:

- l. 669: the word dispersal may not be adequate here (movements instead?)
- l. 681-682: changes in behaviour
- l. 682: “when birds leave the colony…”: the timing is not very clear here (changes between what and what?). Please clarify.
- l. 687-688: given that behaviour is here studied through activity patterns, these two questions seem redundant. Maybe focus on differences between life-stages first and then changes within stages.
- l. 689-690: this remark is a bit strange here, maybe simply refer to the period during which instruments allow recording?
- l. 697: “and increasing number and duration of flight bouts” (or rewrite for coherence)
- l. 698-699: not clear what “changes in activity following fledging” are and what they refer to later on in the study. Consider removing this part of the data (i.e. the fledging period), since it will of course be characterized by major changes but of no specific relevance here?
- l. 700: some capacities? what does this mean?
- l. 794-797: I was a bit confused here as the information seemed contradictory (raw immersion data were obtained from testing every 3 s rather than 30 s; at first I thought that the maximum value could be 20 and not 200). Please rewrite.
- l. 797-799: quite redundant, could be simplified.
- a naïve question: how were GLS fixed on the birds? The corollary question being: when birds are sitting on water, does the GLS automatically get wet? I am wondering whether a distinction can be made between a bird diving to catch food and a bird resting on sea (i.e. not flying), but is this distinction relevant here? (depending on the foraging biology of the birds)
- l. 812-814: please give the meaning of PTT and describe the method here – were PTT attached to GLS? not clear to me how this data was collected.
- l. 873-876: not clear to me here; the issue of unbalanced sampling between sex and stage categories should not constrain a continuous size covariate? Please clarify.
- Table 1: is dispersal again the right term for immatures here?
- Fig. 1 and 2: it would be good to add the raw data on the figures too, not just the model estimates.
- l. 944-946: a sentence very hard to follow, please rewrite (the “while… departure” part fo the sentence seems to be unconnected to the rest of the sentence).
- l. 950: but when do we know whether juveniles exhibit similar behaviour to immatures or adults, if there is no formal test that the curves do not differ anymore after an initial period? (see main comment above). The comparison shown on fig. 12b is interesting, but should it not be statistically supported rather than remaining a simple visual comparison?
- l. 953-954: I do not think that the bell-shaped curve seen in months 15-16 after fledging suggest a behavioural change within the first two months. The sentence needs rewriting (at least, remove “together”?)
- l. 956-958: any suggestion about what these changes may reflect, if not a change in performance?
- l. 972-973: replace “lower performances” by “differences”
- l. 980: “and that shortly after”: please rewrite
- l. 988-990: any explanation for the difference between this species and others?
- l. 1011 and 1016: repetition “in seabird species”
- l. 1027: remove “it”
- l. 1040: rewrite (shorter what?)
- l. 1048-1054: not clear here which sex is concerned. Consider rewriting for clarity (or delete since this is not the main question of interest – see main comments)
- l. 1057: more subtle than what?
- l. 1060-1062: seems largely out of scope here (differences between species, which ones?): delete?
- The conclusion, being merely a summary here, does not seem needed as it does not bring any additional thought here and simply repeats the main results again.

To finish with, please have a check throughout the text to correct English mistakes, there are a number of mistakes / typos to fix, among which those in the list below (on top of those also mentioned by the reviewer):

- l. 632 : remove final parenthesis
- l. 643: hypothesis
- l. 687: behave
- l. 689: do
- l. 699: wandering albatross fledglings
- l. 772: replace by “secondly” or “in a second step”?
- l. 773: “juvenile and adult patterns” or “patterns for juveniles and adults”
- l. 798: the proportion of time
- l. 849: variables
- l. 849: we ran separate models
- l. 870: measurement (or “each of the…”)
- l. 882: in the Amsterdam albatross (or albatrosses)
- l. 896: add a comma after departure
- l. 906 (see also l. 1129): juvenile Amsterdam albatrosses or Amsterdam albatross juveniles
- l. 907: for all three activity variables considered – also specify more clearly that the sex effect was found only for PC2 and PC3.
- l. 967: delete “among”
- l. 969: the same
- l. 1057: “some a trade-offs in duration and numbers”: clearly needs rewriting!
- l. 1071: female Amsterdam albatrosses or Amsterdam albatross females
- l. 1121 and 1129: variation in activity…
- l. 1158: i.e. instead of e.g

Reviewed by **Juliet Lamb**, 19 October 2022

Download the review

Evaluation round #1

DOI or URL of the preprint: `https://biorxiv.org/cgi/content/short/2021.10.23.465439v1`

Authors’ reply, 01 August 2022

Please see attached complete pdf file including:

1) the response to the reviewers,
2) the revised manuscript and the supplementary without the track changes,
3) the revised manuscript and the supplementary with the track changes.

Download author’s reply

Decision by **Blandine Doligez**, posted 24 January 2022

Revision needed

Dear authors,

My apologies for the delay in sending the decision.

Two reviewers have now read your manuscript and provided very detailed and thorough comments on it. Both found the study very interesting and of high potential merit, based on impressive data, but they raised important concerns about both the framework of the study (hypotheses tested) and the meaning of the results (how to demonstrate improvement?), as well as other aspects regarding the analyses themselves and the presentation and discussion of the results. I concur with their concerns and believe that these constructive comments will greatly help in preparing a revised version and improving the manuscript.

Below a few additional /complementary comments:

- l. 26-28: the 'body-size hypothesis with respect to sex differences' is not presented before, and although I can somehow figure out what this means, I think it would be good to clarify what you mean here.
- l. 48: is it not 'resulting from' rather than 'resulting in'? At least here you observe the change of behaviour and interpret it in terms of underlying improvement in foraging skills
- l. 52-54: I believe this is also the case in smaller species, even though this has been documented in fewer cases. Some examples in passerine species that may be worth considering and citing here for comparison and opening perspectives: https://bioone.org/journals/ardea/volume-96/issue-2/078.096.0204/Post-Fledging-Range-use-of-Great-Tit-Parus-major-Families/10.5253/078.096.0204.full, doi:10.1093/beheco/arr063, https://www.sfu.ca/biology/wildberg/NewCWEPage/papers/BoyntonetalCondor2020.pdf, https://ir.lib.uwo.ca/cgi/viewcontent.cgi?article=7954&context=etd, https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.2041-210x.2012.00259.x or https://www.zora.uzh.ch/id/eprint/102335/)
- l. 94: hypothesis B and then C and D are presented before hypothesis A (l. 115). Please adjust?
- l. 136, 142, 144: is dispersal the right term here, given that the movements considered to not lead to settlement for breeding? These seem to be foraging trips rather than dispersal movements.
- l. 170: please consider rewriting here the explanation of immersion data (before presenting the data distribution itself)
- l. 202-205: not clear to me. Please explain
- l. 205-208: the reason for such a two-step process needs to be explained: why not directly testing a stage effect ?
- l. 237-239: is this important here? If yes, why not show full stats and information on distributions?
- l. 303: 'timing of the year': consider rewriting ('with a different timing in the year, i.e. according to month of the year')
- discussion: the discussion of sex differences but also molt patterns seems a bit over-detailed with regards to the main objectives of the study. Not much is indeed discussed about potential sex-related differences in (nor influence of molt patterns on) ontogeny of foraging behaviour. Consider shortening this last part on sex differences and molt patterns, or focusing it on the differences in the dynamics of behaviours with time from departure?
- also, a conclusion about the findings with regards to the ontogeny of foraging behaviour would be welcome here; in particular with regards to the discussion needed about the validation of the changes observed as reflecting an improvement of foraging efficiency (see reviewers' comments).
- throughout the text, please check out grammar to correct mistakes /remove extra words (e.g. l. 379-380).

Reviewed by **Juliet Lamb**, 07 December 2021

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Reviewed by anonymous reviewer 1, 23 December 2021

Within this manuscript Delord and colleagues look to investigate whether foraging behaviour changes both as individuals develop and whether these developmental pathways differ between sexes. The authors conclude that, consistent with previous studies, at-sea foraging and flight behaviour is honed through experience and is also influenced by body size which, in turn, might drive sexually dimorphic foraging strategies in Amsterdam albatross. Whilst the data used in this manuscript are impressive, the potential of the analyses conducted is apparent and the focus on early-life ontogeny is interesting, I nonetheless have some concerns about this manuscript that I would be grateful if the authors could address. I have 5 main in-principle points, and have also some minor comments which I have included below and can be addressed line-by-line.

My principle concern is that it is very difficult to assess 'improvement' in behavioural performance when the authors are a) unable to measure the output of the behaviour (for example the success rate when foraging, or the efficiency of flight) and b) are unable to say what the maximand of a given behaviour is with regards to the quantities measured. As an example, I would suggest that very little time spent in flight could be interpreted as a consequence of highly efficient flight, since if destination is constrained then less flight is indicative of efficient flight, or could equally be interpreted as highly inefficient flight as birds have to take more rests and do more feeding. Therefore, my concern is that without measuring the output of the behaviour, be it flight efficiency or foraging success, it is extremely difficult to say whether changes in behaviour reflect 'improvement' or simply reflect different behavioural maximands between juveniles and adults.

To investigate whether behaviour improves then previous studies, such as Sergio et al., 2014, Thorup et al., 2003 or Wynn et al., 2020, make a prioripredictions as to how a bird would be expected to behave to maximise performance in a specific task. For example, in the Thorup et al. study the authors sought to assess how much birds drifted with the wind, with the expectation that improvement through learning should lead to reduced drift. However, it is unclear to me whether the changes in behaviour reported in the manuscript reflect such improvements in performance or simply reflect differing behavioural objectives between juveniles and adults. This would be particularly true if adults had specific requirements related to breeding that juveniles do not, which I believe has been reported in many procellariform species? I suggest, therefore, that either the authors re-frame their manuscript to reflect this ambiguity, or instead change the analyses somehow to determine whether changes in behaviour really do reflect changes in performance.

My second comment is made with regard to the inclusion of sex as a variable in the models. The authors suggest that sex is included as a proxy for body size owing to the sexual dimorphism seen in Amsterdam albatross. However, as alluded to in the first paragraph of the results it appears that the authors have measurements for body size for all birds. I am unsure, therefore, why sex is included in the model when the variable that the authors suggest sex explains, i.e. body size, is not? I would've thought that including body size, even in a post-hoc analysis, would be inferentially powerful when considering the conclusions drawn.

My third comment is in regard to the analyses undertaken. These complex GLMM-type analyses are not my strong suit, but I do find it confusing as to why the authors assessed some models using AIC comparisons and others they tested for statistical significance. As I say I am no expert, but it seems strange to assess the goodness-of-fit of different models using different methods. Further, I have not come across AIC comparisons between models with different response variables, is this is standard practice? If so some citations to this effect would be useful. Further, I couldn't find how the authors were testing for statistical significance in these models. I have seen in the past the use of likelihood ratio tests when considering these complex mixed-effects models, is that what is used here? If so, I feel that this is worth including in the methods, and similarly it would be nice to see some test statistics and p-values in the results section. Finally, I notice in the supplementary files that some models seem to use the inverse sine square root of the variable (unless I am

misinterpreting asin(sqrt())incorrectly?), yet there isn't a mention of this in the main text. If this is a misinterpretation on my part, I suggest the authors might wish to amend the supplementary files, and if not then they might wish to include in their manuscript a note (and perhaps a citation) on why these transformations are used?

My final comment is that parts of the discussion strike me as fairly speculative and could be shortened considerably (perhaps even removed?) without detracting from the message of the main text. I have included in my line-by-line comments instances where this seems to be the case, and I suggest that the authors may wish to 'streamline' the discussion (and in doing so make the paper more appealing to the casual reader?) or, alternatively, include more information so as reduce how speculative this section is.

I hope the above comments prove useful. As I say I think the questions asked by this manuscript are important, and the data is impressive, though I believe that addressing the above points will improve this manuscript considerably. Below, I've included some line-by-line comments on the manuscript as a whole.

Minor comments
Lines 39-51: the authors might consider introducing the concept of 'learning' in slightly greater detail (given that learning is central to the hypotheses explored). Learning often refers to stimulus-response associative learning ('trial and error'), though when considering the ontogeny of complex behaviour as discussed then other forms of learning (such as social learning or imprinting) are also considered. It could be of interest, and could improve clarity, then to say what learning actually means in this context.

Line 81: What sort of logger is used? This is elaborated on later, but should really be included here (first mention).

Line 105: Do you mean the Table S1? I don't think that table 2 includes the hypotheses predictions mentioned.

Line 125: Citation needed?

Lines 135-152: unclear why this is in the methods? Seems like a literature review, perhaps better in the introduction?

Lines 195 onwards: the response variable names are slightly confusing, is worth considering using the long-form names (e.g. proportion of time in seawater rather than PROPWATER)? I appreciate this is a matter of individual taste, though I found myself constantly re-referring to the methods which perhaps made things more confusing.

Line 201: Within the first year 'month since departure' and 'months overall' will correlate perfectly 1:1. How do the authors account for this? Also, month of year is a circular variable (e.g. 12 is closer to 1 than to 6). Do the authors attempt to compensate for this?

Line 211: Visually inspected rather than tested?

Line 217: Why assess propwater using GLMM and the others in an AIC framework? If all have different response variables this is confusing, is there a precedent for this approach?

Line 237: Are there confidence intervals, p-values and test statistics for this? More generally, every use of the word significance should probably have a test stat and p-value.

Line 243: "Juveniles showed strong temporal changes linked to the time elapsed since departure from the colony." Does this just mean that behaviour changes as time since fledging increases?

Line 318: Do the results really suggest that performance improvement is occurring? Given you have no resolution regarding flight performance (i.e. range and efficiency) or feeding performance (i.e. food capture probability) its surely quite hard to conclude that birds are getting better at anything. It shows changes, yes, but improvement? Not sure.

Line 319: What does 'movement performance' mean?

Line 325: For the reasons mentioned above I'm not sure that this is 'very likely' to reflect improvement in feeding? More generally I'm not sure that 'very' is a useful word here, given that it's inherently slightly subjective.

Line 326: Whilst this is true, within-area variance in oceanographic quality, which given the non-tropical distribution could be very high, could still drive trends. Given you have spatial information from the GLS in the form of light level data could this not be specifically tested and accounted for? I feel that this point would be a lot stronger if geographic position were accounted for.

Line 329: Can argue that change often equates to improvement (e.g. Campioni et al. 2020) but plenty of examples where behaviour changes reflect changes in maximand rather than improvement in performance. I'm not sure it's valid to suggest that simply because birds become more 'adult like' in their foraging/flight patterns they must be improving?

Line 336: "Additional skills need to be required". This is fundamentally a manuscript about learning. How do the authors suggest that learning occurs?

Line 353: If sex is included in the model as a proxy for body size, yet you have body size upon departure, why not include body size instead?

Line 365: Cite?

Line 373: What are birds waiting for in a 'sit and wait' strategy?

Lines 362-395: This feel very speculative and not very relevant to the overall focus on ontogeny, consider removing perhaps?

Line 412: Does this relate to the results presented in this manuscript or to existing data? Not clear from the text.

Line 418-437: Again, given the limited data from the focal species this para feels very speculative?

Line 438: Perhaps include a conclusion?

All figures: Why are error bars only on one side of the point?