PCI PCIEcology

Decision concerning your submission

Dear Karine Delord,

Your article, entitled “The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird”, has now been reviewed. The referees' comments and the recommender’s decision are shown below. As you can see, the recommender found your article very interesting but suggests certain revisions.

We shall, in principle, be happy to recommend your article as soon as it has been revised in response to the points raised by the referees.

When revising your article, we remind you that:

1) Data must be available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad (to pay) or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data;

2) Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) must be available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused;

3) Details on experimental procedures must be available to readers in the text or as appendices;

4) Authors must have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this article declare that they have no financial conflict of interest with the content of this article.";

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We thank you in advance for submitting your revised version.

Yours sincerely,

The Managing Board of PCIEcology

article picture

The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird

KARINE DELORD, HENRI WEIMERSKIRCH, CHRISTOPHE BARBRAUD

https://biorxiv.org/cgi/content/short/2021.10.23.465439v1 version v1

Submitted by Karine Delord 26 Oct 2021 07:51

Abstract

The transition to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher mortality including that of inadequate/inferior foraging skills compared to adults, young naive individuals combining lack of experience and physical immaturity. Thus a change in behaviour, resulting in an improvement of skills acquired from growing experience, is expected to occur during a period of learning through the immaturity phase. Very few studies have investigated the ontogeny of foraging behaviour over long periods of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over several years. We investigated the foraging behaviour, through activity patterns, during the successive life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naive juveniles, immatures and adults. Juvenile naïve birds during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, higher duration and more numerous bouts on water, and lower duration and less numerous flying bouts). Juveniles reached similar activity values to those of immatures and adults as early as the 2nd-3rd months since independence, suggesting a progressive improvement of foraging performances during the first two months since fledging. We found support for the body-size hypothesis with respect to sex differences in activity parameters according to time elapsed since departure from the colony and month of the year, consistent with the important sexual dimorphism in the Amsterdam albatross. Whatever the life stage considered, activity parameters exhibited temporal variability reflecting the modulation of foraging behaviour possibly linked to both extrinsic (i.e. environmental conditions such as variability in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew during moult) factors.

Keywords: activity data loggers; foraging behaviour; southern Indian Ocean; Amsterdam albatross; Diomedea amsterdamensis

Round #1

by Blandine Doligez, 24 Jan 2022 20:38

Manuscript: https://biorxiv.org/cgi/content/short/2021.10.23.465439v1

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.

R: We would like to thank the reviewers for their useful comments and the editor for allowing us to resubmit a revised version of our work. We have done that revision by closely following the reviewers' recommendations.
Further details are given below where we carefully address all major and minor concerns raised by the reviewers.

Please note that due to the extent of the changes in the revised version, we have chosen to include in the revised document submitted for ease of review process:

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

NB: the lines indicated in the responses to reviewers refers to the version with the track changes

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.

R: this was rephrased in the revised version (L24-31)

- 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

R: thank you, you are right, this has been changed accordingly (L50)

- 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/)

R: thank you for your useful suggestions regarding smaller species. In the revised version we included several of your suggested references (L52-59)

- l. 94: hypothesis B and then C and D are presented before hypothesis A (l. 115). Please adjust?

R: this was adjusted in the revised version of the main manuscript (L106-140) and in the Table S1

- 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.

R: this was reworded as migratory movements and a reference was added (L174, 180, 182)

- l. 170: please consider rewriting here the explanation of immersion data (before presenting the data distribution itself)

R: sorry, we are not sure to fully understand your comment here. Nonetheless, we rephrased related sentences in the previous paragraph mentioning immersion data (L192-207; 210-211)

- l. 202-205: not clear to me. Please explain

R: we added an explanation in the revised version (“*Month elapsed since departure (the duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on) were used to test for time variation in activity parameters*”; L277-279)

- l. 205-208: the reason for such a two-step process needs to be explained: why not directly testing a stage effect ?

R: the modelling procedure was completely changed following the recommendations made by one of the reviewer, Juliet Lamb. Consequently, the Material & Methods and Results sections were modified. We think that the new methodological approach has improved the manuscript and addressed the comments made by the reviewer.

- l. 237-239: is this important here? If yes, why not show full stats and information on distributions?

R: we think presenting results on sexual size dimorphism is helpful to interpret activity data and differences between sexes. Following your recommendation we thus present full stats related to sexual size dimorphism (Tables 6-12)

- l. 303: ‘timing of the year’: consider rewriting (‘with a different timing in the year, i.e. according to month of the year’)

R: this was changed accordingly

- 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?

R: following your comments and those from reviewers the Discussion section was largely rewritten (restructured, over-details removed or moved to supplementary)

- 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).

R: a conclusion was added in the revised version

- throughout the text, please check out grammar to correct mistakes /remove extra words (e.g. l. 379-380).

R: we checked carefully for grammar and mistakes

Reviews

Reviewed by Juliet Lamb, 07 Dec 2021 12:52

Download the review

Review: Delord et al., *The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird*

This study presents wet-dry patterns recorded by geolocators on Amsterdam albatrosses at different life stages. The authors use these patterns to infer differences in foraging behavior among life stages, sexes, and individuals. The study allows for direct comparisons between juvenile, immature, and adult life stages tracked over multiple months, which is relatively unique.

Although the questions raised are interesting and the dataset is comprehensive, some aspects of this article feel more like an exploratory analysis than a finished product. From a single binary measurement (whether a sensor is wet or dry), the authors derive five very similar, interrelated metrics (% time on water, number and duration of wet bouts, number and duration of dry bouts), which are then analyzed independently to infer essentially the same behavior (foraging). Given that similar and overlapping interpretations are offered for these metrics, this gives an overall impression of unnecessary redundancy. In addition, the authors make extensive and sometimes contradictory assumptions about the meaning of the wet-dry patterns they observe. For example, they interpret differences in wet-dry patterns between juveniles and adults to represent decreased foraging success/efficiency during the juvenile period, but interpret similar differences between sexes in adults to represent different foraging strategies (foraging-

in-flight vs. sit-and-wait). Thus, the results often feel repetitive, and the interpretations strained. A more effective approach might be to use multivariate analysis to evaluate whether distinct foraging behaviors can be detected across the various aspects of wet/dry dynamics, and then to evaluate how use of these strategies varies over time and among individuals.
Aside from the general approach, I also had concerns about the framing of the study, analysis and interpretation of results, sample sizes, and figures, which I will discuss in turn.
R: we warmly thank the reviewer for taking time to provide these insightful comments. Following your recommendations we used a new analytical approach in the revised manuscript. First, we performed a multivariate analysis by combining the five metrics obtained from the wet/dry sensor in a principal component analysis. This resulted in three main independent axes that explained 94.2% of the total variance and which we could easily interpret in terms of types of behaviors. This procedure ensured that these three new metric (PCA axes) were independent and not correlated, therefore avoiding redundancy. It also reduced the number of metrics used to describe behavior, which simplified some parts of the manuscript and facilitated interpretations. In a second step, we used each of the three metrics as independent variables and tested for the effects of explanatory covariates (months elapsed since departure, stage, month of the year, sex) using generalized additive mixed models which considered different types of random effects (no random effect, random intercept, random intercept and slope). Further details are given below and in the revised manuscript. We are convinced that this new analytical approach is more robust and considerably improved the quality of the manuscript, and thank you for these useful suggestions.

Framing:
The introduction does not effectively contextualize most of the hypotheses presented in Table S1, instead focusing entirely on the juvenile stage. Thus, there is no context for the importance of moult (and nature of predicted seasonal changes), importance of the immature period, and predicted sex-based differences presented in the hypotheses and in the discussion. At the same time, given the wide variety of studies on foraging and movement in juvenile seabirds and other birds described in the Introduction, the novelty of the study's central findings is not especially clear.

R: according to your comments the Introduction section was partly modified. We paid more attention to clarify the novelty of this study and to present contextual elements regarding moulting constraints and patterns (L91-93, L126-134). Table S1 was revised following comments from the editor and the other reviewer

The authors present several unknowns in the introduction that are not tested as part of this study, including whether decreased foraging efficiency contributes to juvenile mortality and which processes (e.g., learned experience vs. physical development) are responsible for post-fledging changes in foraging behavior. Focusing on these questions gives the misleading impression that they will be addressed in the manuscript.

R: in the revised version we modified the Introduction trying to be more specific about the concepts and hypotheses which are tested in the manuscript.

The authors emphasize the longitudinality of their study and mention multi-year data, which initially led me to believe that individual results would span multiple life stages and/or years. In fact, the groups for each life stage are composed of different individuals, comparison among the three groups is only possible for the first 10 months post-departure, and individual trajectories are not directly mentioned or analyzed. If the main goal of the paper is to make comparisons among life stages/seasons, I would suggest focusing on this aspect of the work rather than on individual longitudinality; otherwise, results related to individual changes over time should be presented.

R: our main goal was to make comparisons among life stages and seasons based on activity data collected during the first ten months post-departure, as this is the common period to all stages to allow comparisons. For juveniles, an additional goal was to determine changes in activity patterns during the first two years of life for which we had data. To clarify this we reworded and added a sentence in the Introduction and Discussion sections (L91-93, L472-478).

Analysis/interpretation of results:

A particular strength of this study would appear to be the multi-year data obtained from juveniles, but (as far as I can tell) the authors do not use these data to compare behavioral changes within individuals between subsequent years. The one exception is in Figure 6, which compares juvenile behavior 15-16 months post-departure with immature/adult behavior immediately after departure; however, it is not clear why this particular time lag is suggested or how to interpret it.

R: indeed juvenile is the only stage for which we have multi-year data. As you rightly pointed out we present behavioural changes for juveniles during their first two years in figures S8 - S12, but we also compare behavioural changes (from a statistical point of view) as shown in tables 5, S4.

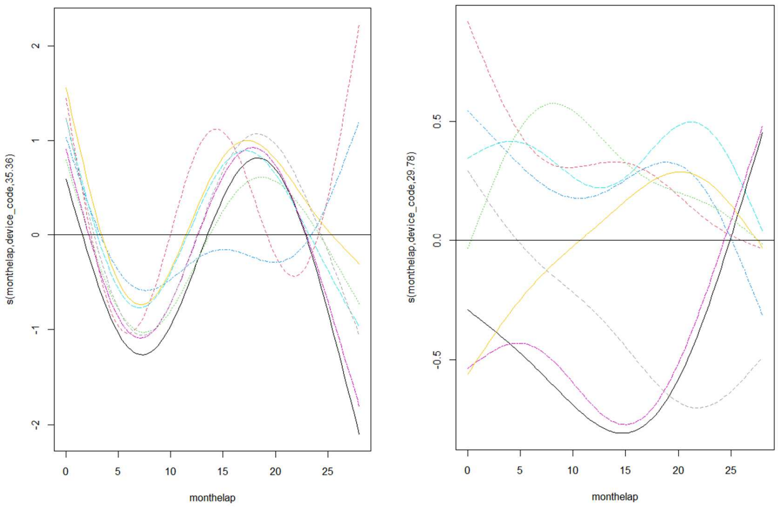
Since juveniles leave the colony in January and the breeding season starts in March with the laying of the egg, the lag of 15-16 months post-departure that appear in figure S12 shows the activity of adults and juveniles from the start of the following breeding season when juveniles reach 2 years old.

The difference in tracking duration between juveniles (2 years) and immatures/adults (1 year) also raises the question of how the second year of data in tracked juveniles was treated, since behavior appears to be very different during Year 2 after departure compared to Year 1. Were both years combined in other analyses (e.g., month-of-year) and, if so, why? Why not present direct comparisons of Year 1 and Year 2 for juveniles?

R: as mentioned in response to the above comment, direct comparison of year 1 and year for juveniles was performed and results shown in supplementary tables. We did not compare years, but months in order to have a finer grained description of the changes month by month. Now, when comparing juveniles with the other stages (adults and immatures) we only compared activities during the first 10 months after departure from the colony, as our aim was precisely to compare the stages. Thus, the second year of data for juveniles was not taken into account when comparing juveniles, immatures and adults.

Individual variability is mentioned in the Methods in reference to the use of mixed models, but results are not presented or discussed. Given that the intercept terms in the models are significant, it seems as though individual variability (i.e., specialization on different foraging strategies) could be a contributor to observed variability. It would be interesting to know more about this, including whether and at what rate intra-individual variation in foraging strategies decreases or stabilizes during the juvenile period (which would suggest development of specialized individual foraging behaviors). Given the small sample sizes, the degree of individual specialization could influence results and limit extrapolation.

R: we now present more details about individual variability in the Results and discuss these results. To test for differences in the rate of intra-individual variation in foraging strategies we also considered models with random slopes. We thus compared models without random effect, with a random intercept and with a random slope in this revised version and selected the best model based on AIC, which was then used for testing fixed effects (L277-289). Below an example of models outputs obtained when modelling the variation in activity (PC1 and PC2, see below) as a function of the number of months elapsed since departure and with random intercepts and slopes (each coloured line representing an individual) and now included in the revised version supplementary (Figure S7).



Similarly, individual trajectories are not analyzed, and months since departure are treated independently rather than as a continuous process. I would expect (at least in juveniles) some evolution in foraging strategies over time, but the present analyses are not sufficient to detect such changes on the individual level.

Month of year is a rather arbitrary way to analyze seasonal changes, especially since months are considered categorically. A more useful approach might be to use time as a continuous covariate and fit a non-linear function (e.g., quadratic) to better show changes over the annual cycle, or to select ecologically meaningful seasons within which relevant environmental covariates (wind, sea surface temperatures, presence of fronts/eddies, etc.) are relatively consistent in the study area.

R: this is a good point and in the revised manuscript we performed new analyses where month since departure was treated as a continuous process. More precisely, we performed generalised additive mixed models where month since departure was modelled with smoother and where the effects of stage, sex, and month of the year were treated as fixed effects. As explained above we also considered models without an individual random effect, models where individual identity was considered as a random effect (random intercept models), and models where we allowed individual variation in the rate of change of activities according to the month since departure (random intercept and slope models) (L277-289).

Although linear modeling results show significant differences in many of the tested covariates, the ecological relevance of these differences appears to be relatively weak (coefficient values of <0.5 for most parameters). Such differences might be expected given the large sample sizes of wet-dry bouts (numbering in the thousands) and high within-individual replication. The figures also seem to show large variance and high overlap among life stages across all response variables. Some discussion of effect size and whether observed differences are ecologically meaningful is warranted.

R: following your previous comment the M&M and Results sections were entirely rewritten (L240-446)

In the text, adults and immatures are typically presented as a single group (in contrast to juveniles). However, the figures and some results suggest that immatures may differ from both adults and juveniles in some aspects of their behavior. It would be useful to include some discussion of these differences, and of the immature life stage in general.

R: following your comments analyses were changed and a paragraph was added on comparison between immatures and juveniles/adults in the Discussion section L480-598

The Abstract states that juvenile foraging behaviors are similar to adults within 2-3 months post-fledging, while the Discussion asserts that they do not become similar until 10-17 months post-fledging. I am not sure where the 10-17 months figure comes from (since direct comparisons are only possible through Month 10). I assume this is related to the 15-16 month offset shown in Figure 6, but I have no idea what this offset means, why it is different for adults vs. immatures, how it interacts with seasonal patterns, etc. Arbitrarily comparing one aspect of adult/immature post-departure behavior to juvenile behavior more than a year later does not allow for any conclusions about whether juveniles are behaving similarly to adults/immatures at that time. In any case, some clarification is needed about which figure (2-3 months or 10-17 months) is correct, as well as where the 10-17 month value comes from.

R: following your comments this was clarified in the Abstract

Sample sizes:

It is unclear what the sample sizes were for male-female comparisons within each life stage, since sex ratios are not given. As sample sizes were small for all life stages (10-13 individuals per stage), this suggests that sex-specific samples by stage could have consisted of only a few individuals.

R: the sex ratio was added in the revised version (Table 2). As you rightly mention, the sample sizes are small, directly related to the fact that the population is very tiny with ~40 pairs breeding annually and a maximum of 30-35 fledglings per year.

Other sources of variability (e.g., differences in departure dates and bimodal distribution of departures in adults) could also affect observed patterns, especially if they differed between sexes. Some discussion or analysis of how departure dates are distributed, as well as how time since departure interacts with annual-cycle patterns, would be warranted.

R: as previously mentioned sample sizes are small, all the more so if we want to compare the sexes, making the analyses poorly robust. Thus, we could not include other sources of variability such as departure date in the models.

Regarding the chronology of departure dates (month of the year) by stage we have the following pattern (number of individuals is indicated):

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
juvenile	5	2	1	0	0	0	0	0	0	0	0	0
immature	0	0	0	1	5	3	3	1	0	0	0	0
adult	4	6	0	0	1	2	1	0	0	0	0	1

Although sample sizes are small, juveniles and adults appear to leave the colony in January and February (which is totally expected since this is the end of the breeding period), and immatures appear to leave the colony between May and July.

Figures:

The figures themselves are very monotonous, and many of the results highlighted by the authors are not readily apparent from looking at the figures alone given the very large variability and relatively narrow range of variation in averages among months.

R: according to your comments all the figures were changed in the revised version

Most of the figures focus on male-female differences, while most of the discussion focuses on comparison among life stages. Understanding how and whether life stages differed from one another requires mentally superimposing the subfigures, which is tricky to do.

R: following your comments the figures in the main manuscript were modified in the revised version to facilitate comparison among life stages

Minor comment: in Figure S4, the juvenile values appear to be the same in both subfigures.

R: thank you, the mistake was corrected and the figure modified in the revised version

Reviewed by anonymous reviewer, 23 Dec 2021 11:37

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 priori predictions 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.

R: we understand your concern about the output of the measured behaviour and our data do not allow obtaining an objective measure of the output of the different behaviours at sea (such as foraging success as you suggested or for example body condition). We therefore agree that it is difficult to make inferences on improvement from the analysis of differences and variations in activities between stage and individuals. Therefore, following comments from the Editor, yourself and of the other reviewer, and given that the activity data (from GLS) available to us do not allow to perform analyses comparable to those you mentioned in Thorup et al. (2003) for example, we have rewritten many parts of the manuscript, focusing on behavioural differences and changes, and not on performance improvements.

As you rightly mentioned it is well known in seabirds that breeding adults have specific energy requirements linked to reproduction and central place foraging. For this specific reason and in order to compare juveniles, immatures and adults without this bias, we carefully selected the data for adults and we have discarded all data that could be related to the reproduction period.

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.

R: we agree that sex and body size covary, as for all body size measurements males and larger than females. However, in less dimorphic species and even in monomorphic species, sexes may differ in their foraging tactics and parameters. This is why we included sex as a covariate and not body size. In the revised version we initially attempted to add body size as an additional covariate but we realised than sample sizes for each sex and stage categories were small and unbalanced, which gave us poor confidence in the results. In fact, due to these small sample sizes, sexual size dimorphism was not significant when tested for birds for which we had GLS data, whereas it was clearly significant when tested on the whole dataset included all the measured birds in our database. We thus present data and test about body size differences between sexes and stages based on the entire database, and discuss the potential role of body size in explaining behavioural differences between sexes and stages.

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?

R: following your comments and those of the other reviewer we completely modified the section by changing the modelling process in the revised version (please see below for detailed changes L236-330). To make inferences we used model selection based on AIC comparison between competing models. Note that following suggestions made by reviewer 1 we used a new analytical approach in the revised manuscript. First, we performed a multivariate analysis by combining the five metrics obtained from the wet/dry sensor in a principal component analysis. This resulted in three main independent axes that explained 94.2% of the total variance and which we could easily interpret in terms of types of behaviors. This procedure ensured that these three new metric (PCA axes) were independent and not correlated, therefore avoiding redundancy. It also reduced the number of metrics used to describe behavior, which simplified some parts of the manuscript and facilitated interpretations. In a second step, we used each of the three metrics as independent variables and tested for the effects of explanatory covariates (months elapsed since departure, stage, month of the year, sex, body size) using generalized additive mixed models which considered different types of random effects (no random effect, random intercept, random intercept and slope). Further details are given in the revised manuscript.

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.

R: the Discussion Section was largely rewritten in the revised version according to your comments and to the other reviewer comments (please see details below). We shortened the discussion and reduced speculations accordingly.

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.

R: we thank the reviewer for the positive and constructive comments on the ms. Accordingly, we followed the suggestion to modify the structure in the revised version of the ms detailed below.

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.

R: according to your comment a sentence was added to introduce the concept of learning L52-54

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

R: as suggested we added details on the sort of logger that was used (1st mention) here in the revised ms

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

R: this was revised accordingly throughout the Introduction section

Line 125: Citation needed?

R: citation was added (L162)

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

R: we chose to include this paragraph summarising results obtained from previous tracking studies on the Amsterdam albatross in the Method section to justify why we focused on activity data in our study (not considering spatial aspects of the at sea distribution). Nevertheless, if the reviewer prefers that we move this paragraph because it suits better in the Introduction section, we would be happy to reconsider it.

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.

R: following your suggestion the acronyms were changed for the long-form names throughout the revised version

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?

R: in our new analytical approach using generalised additive mixed models, month elapsed since departure was considered as a continuous variable to investigate how individuals changed their behaviour following their departure from the colony. This allowed testing for non-linear relationships. In these models month of the year was used as a categorical variable with the aim of comparing how behaviors differed on a seasonal basis. Although there is a correlation between these two covariates during the first year, this is not the case after and according to their stage individuals do not leave the colony the same month of the year (juveniles and adults leave in January and February, whereas immatures leave between May and July).

Line 211: Visually inspected rather than tested?

R: this has been changed in the revised version due to the new analytical approach

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?

R: as explained above, the statistical analyses section in the revised manuscript was completely rewritten according to the changes suggested in the modelling process (PCA and GAMMs, please see L236-309)

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.

R: the statistical results (tests and p-values) were presented in the Tables 7-12, this is now more clearly indicated in the revised version

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?

R: yes, it does mean that, this was added in the revised version to clarify (L334-457)

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.

R: the Discussion section was largely rewritten regarding all your comments on performance improvement interpretation (L466-489, L566-585)

Line 319: What does 'movement performance' mean?

R: the Discussion section was largely rewritten regarding all your comments on performance improvement interpretation (L445-520, L566-604)

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.

R: this has been tempered accordingly in the revised version (L505-509, 600-604)

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.

R: since the aspect of habitat selection and spatio-temporal segregation between life-stages was extensively described and analysed in previous studies (cited in the manuscript), we wished to focus here only on the temporal dataset of activity parameters to explore this specific question. We understand that this can be frustrating. However, in order not to dilute the message of the present manuscript, we prefer not to include this aspect in this study.

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?

R: the Discussion section was largely rewritten regarding all your comments on performance improvement interpretation (L465-702)

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

R: we briefly indicate examples of such skills (detection of prey at the surface, detection of other foraging seabirds, navigational skills…) L534-535

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?

R: see our response above about including body size as an additional covariate in the models.

Line 365: Cite?

R: reference added L661

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

R: like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface. Additional details on likely preys were added in the revised version (L146-158)

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

R: according to your comments this was rewritten. The descriptive parts were moved in the Method Section

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

R: this was rephrased and references were added in the revised version

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

R: according to your comments this paragraph was shorten and partly moved to the Supplementary. As moulting is an important parameter which can induce behavioural changes and which has strong energetic implications, we wished to keep a reduced paragraph on this theme, even if it may seem speculative (L628-647; Supplementary L35-52)

Line 438: Perhaps include a conclusion?

R: according to your comments and those of the other reviewer a conclusion was added (L704-720)

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

R: we have chosen to illustrate error bars by only one side bar, to favour clarity and understanding of the figures, because as it was mentioned by reviewer #1 results exhibited a very large variability. However, if you feel it is better to modify it according to your suggestions we will be happy to modify them.

TITLE

The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird

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Abstract

The transition to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher mortality including that of inadequate/inferior foraging skills compared to adults, young naïve individuals combining lack of experience and physical immaturity. Thus a change in behaviour, resulting in an improvement of skills acquired from growing experience, is expected to occur during a period of learning through the immaturity phase. Very few studies have investigated the ontogeny of foraging behaviour over long periods of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over several years. We investigated the foraging behaviour, through activity patterns, during the three life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naïve juveniles, immatures and adults. Naïve juveniles during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, longer and more numerous bouts on water, shorter and fewer flying bouts). Patterns of activity parameters in juveniles after independence suggested a progressive change of foraging performances during the first two months since fledging. We found sex differences in activity parameters according to time since departure from the colony and month of the year, consistent with the important sexual dimorphism in the Amsterdam albatross. Regardless of life stage considered, activity parameters exhibited temporal variability reflecting the modulation of foraging behaviour. This variability is discussed in light of both extrinsic (i.e. environmental conditions such as variability in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew during moult) factors).

Keywords: activity data loggers; foraging behaviour; southern Indian Ocean; Amsterdam albatross; *Diomedea amsterdamensis*

Introduction

The transition from parental food dependency to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals (Mushinsky et al. 1982; Margrath and Lill 1985; Martin and Bateson 1985; Marchetti and Price 1989; Langen 1996; Burns et al. 2004) and is increasingly documented in a wide range of taxa (reptiles, birds, and some mammals). A widely accepted hypotheses is inadequate/inferior foraging skills of juveniles compared to adults, young naïve individuals combining lack of experience and physical immaturity (Lack 1954; Daunt et al. 2007). Thus, a change in behaviour, resulting from an improvement of skills acquired from increasing experience is expected to occur during a period of learning through the immaturity phase. Learning often refers to stimulus-response associative learning ('trial and error'; Ruaux et al. 2020), although other forms of learning (such as social learning or imprinting) are also taken into account when considering the ontogeny of complex behaviours (Heyes 1994; Wynn et al. 2020). Such a learning process has been studied on various taxa from insects to primates (Bruner 1972; Caubet et al. 1992; Dukas 2006; Rapaport and Brown 2008).

Juvenile birds are known to undertake vagrant erratic journeys during the post-fledging period in passerines (Naef-Daenzer and Grüebler 2008; Becker 2014; Evans 2018; Boynton et al. 2020), in raptors (Urios et al. 2010; Krüger et al. 2014; Harel et al. 2016) and in seabirds (Riotte-Lambert and Weimerskirch 2013; Collet et al. 2020). Recent studies highlighted that the flight capacities and foraging behaviour of juveniles differed from those of adults in storks (Rotics et al. 2016), raptors (Harel et al. 2016; Nourani et al. 2020) or seabirds (Ydenberg 1989; Péron and Grémillet 2013; de Grissac et al. 2017; Corbeau et al. 2020). Most flight components were found to improve over time to tend towards those of adults (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2017; Corbeau et al. 2020).

However, studies focusing on the foraging behaviour of juveniles remain scarce because of the difficulty to obtain individual tracking data for long periods, especially for long-lived pelagic seabirds with deferred maturity. Moreover, existing studies comparing flight capacities and foraging behaviour between juveniles and adults in such species only collected data during the first few months that juveniles spent at sea. Since juveniles may spend several years at sea before returning to a colony to breed, our understanding of the ontogeny of flight capacities and foraging behaviour remains fragmentary.

The Amsterdam albatross *Diomedea amsterdamensis* is a large and long-lived pelagic seabird with an extended immaturity stage (~ 9 years Rivalan et al. (2010)). Similarly to a closely related species, the wandering albatross *D. exulans*, their foraging strategy relies on very low flight costs as a result of their dynamic soaring flight, whereby individuals optimize the orientation of their movement with wind direction to maximize the daily distance covered (Pennycuick 1982). During initial post-fledging dispersal juveniles wander alone over very long distances from their colony. At sea distribution during every stage of the life-cycle of Amsterdam albatross was studied by Thiebot et al. (2014) and de Grissac et al. (2016) who compared flight trajectories (i.e. departure direction or orientation toward specific areas) of juveniles and adults. Both studies concluded on slight differences among stages in distribution due to the extensive area they used. However, foraging behaviour is known to be constrained by intrinsic factors such as sex, age, reproductive status and body size across a wide range of taxa and hence play a key role in shaping activity (King 1974; Alerstam and Lindström 1990; Wearmouth and Sims 2008). To understand the changes in foraging proficiency according to experience (life-history stages), longitudinal studies of individuals spanning critical periods of their lives are thus required. Advances in animal-borne instrumentation enable key component of foraging behaviour such as foraging effort and activity to be recorded over long periods. In this study, we benefited from a unique dataset of different life stages (juveniles, immatures and adults) and a remarkable duration (up to 28 months for juveniles) to characterise and compare the behaviour changes when birds leave the colony for several months (immatures and adults) or years (juveniles). We analyse the foraging behaviour, through activity patterns, of naïve juveniles (first years of independence at sea), immatures (individuals that never bred, age 2-10 years) and adults (individuals that bred at least once, age 8-28 years) of Amsterdam albatross (Table 1). By using miniaturized activity loggers (Global

Location Sensing; GLS) to infer foraging behaviour (activity) throughout the successive life stages we addressed the following questions: i) do individuals belonging to different life-stages behaved differently? ii) are there differences in activity patterns between life-stages, and are there detectable progressive changes? However, the loggers used does not yet allow to have longitudinal data and to cover the entire period until an individual is recruited into the population as a breeding adult, i.e. at least 8 years.

Previous knowledge of the ecology of large albatrosses and Amsterdam albatross described above provides a practical framework for testing predictions about variability in foraging behaviour associated with stage, time elapsed since departure from the colony, seasons and sex which are summarised in Table S1. Given the overlap of spatial distribution between life-stages (not presented here but see Thiebot et al. 2014; de Grissac et al. 2016; Pajot et al. 2021) we predicted that juveniles would compensate for any lack of foraging proficiency by increasing foraging effort and time (i.e. lower time spent on water and longer flying bouts, in other words decreasing time sitting on water and longer and more numerous bouts in flight; Hypothesis (A), Table S1). We also predicted changes in activity following fledging of juveniles from the colony followed by more progressive changes. Based on results found on fledglings wandering albatross (Riotte-Lambert and Weimerskirch 2013; Pajot et al. 2021) showing that juveniles reached some adult foraging capacities in less than two months, we predicted that changes should be detected in activity parameters early after the juvenile left the colony (within few first months). Overall, juveniles should show contrasted foraging effort (i.e. longer time spent on water, shorter flying effort with fewer and shorter flying bouts) just after fledging compared to other life-stages. Due to seasonal changes in food availability individuals will face at sea after leaving the colony and the alleviation of energetic constraints linked to reproduction (for breeding adults) or to alternate foraging trips at sea and period on land for pair bonding and mating display (for immature birds), we predicted that adjustments of activity will occur according to the time spent (i.e. in months elapsed) since the departure of individuals from the colony (Hypothesis (B), Table S1). In juveniles, we predicted early and rapid changes after fledging and then more progressive changes. Due to environmental changes occurring throughout the seasons we predicted temporal (i.e. related to the month of the year) changes in activity parameters for all life-stages (Hypothesis (C), Table S1). Although food availability may be lower during winter, foraging effort may also be reduced when adults and immatures are moulting (Weimerskirch 1991). Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch 1991). Partial moulting is suspected to occur outside the breeding period and to result in reduced activity (i.e. more time spent on the water; Weimerskirch et al. 2015, 2020). We therefore predicted a period of reduced activity that differs according to the life-stages and may be confounded by seasonal variability (Hypothesis (C). Lastly, due to sex differences in flight performances (Shaffer et al. 2001; Clay et al. 2020), specifically, due to their higher wing loading, males should both maintain longer flying effort, and be more likely to minimize the number of flying bouts than females. Thereupon, and based on results on wandering albatross (Riotte-Lambert and Weimerskirch 2013), similar pattern should be maintained outside the breeding period. We thus predicted differences in foraging behaviour between sexes (i.e. time spent on water, duration and number of flying and water bouts; Hypothesis (D), Table S1).

Materials and methods

Study species and data loggers

Amsterdam Island (37° 50’ S; 77° 33’ E) is located in the subtropical part of the southern Indian Ocean. In this oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder sub-Antarctic waters (Belkin & Gordon 1996). Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021; see Supplementary). Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997b). However, this strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014), leading to a more important utilization of the '*sit-and-wait*' technique and possibly to vary depending on sites suggesting behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the former technique (compared to '*foraging-in-flight*').

The Amsterdam albatross, like other great albatrosses, is a biennial breeder (Roux et al. 1983; Jouventin et al. 1989), with high survival during juvenile, immature and adult phase (Rivalan et al. 2010). The adults that raised a chick successfully do not start a new breeding cycle after chick fledging, but remain at sea for a sabbatical period (~1 yr; Table 1; Rivalan et al. 2010). However, early failed breeders may start to breed the following year (Rivalan et al. 2010). Immature birds may visit the colony when they are 4−7 yrs old, but generally only start breeding at 9 yrs old (Table 1; Weimerskirch et al. 1997a). Juvenile birds fledge and migrate independently from the adults in January (Table 1). Exact fledging dates were not known for juveniles but were assessed from activity pattern as juvenile birds land on water quickly after leaving the colony (Weimerskirch et al. 2006). Amsterdam albatrosses were monitored annually since 1983 and all individuals were individually marked (numbered stainless steel and plastic engraved colour bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age (79 individuals since the beginning of the study) and chicks of the year were banded, weighed (body mass ± 50 g using a Pesola®

spring balance) and measured (wing length ± 1 mm with a ruler, tarsus length, bill length, and bill depth ± 0.1 mm with calipers).

Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale migratory movements (*sensu* Weimerskirch et al. 2015a) reaching >4000 km from the colony exploiting continuously warm waters (~18°C). No clear longitudinal seasonality existed in the movements of adults, nonetheless they tended to move westwards in June/July and eastwards in November. The immature birds moved widely in longitude (0° to 135° E), exploiting exclusively warm waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity existed in the movements, except that they also tended to move westwards in June and eastwards in November. Juveniles exhibited very large migratory capacities over the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal gradient (27° to 47° S). Juveniles birds tended to migrate westwards first in March-April and temporarily exhibited synchronous individual movements. De Grissac et al. (2016) compared trajectories (i.e. departure direction or orientation toward specific areas) of juveniles and adults and showed that juveniles performed an initial rapid movement taking all individuals away from the vicinity of their native colony, and in a second time performed large-scale movements similar to those of adults during the sabbatical period. High individual variability and no clear differences between juveniles and adults patterns were found, except that adults foraged at significantly higher latitudes. De Grissac et al. (2016) concluded in an overlap in distribution between adults and juveniles due to the extensive area they used and their differences in latitudinal distribution compared to other Procellariiformes species.

GLS are archival light-recording loggers used to study activity of birds over periods lasting up to ~ 2 years. GLSs record the ambient light level every 10 min, from which local sunrise and sunset hours can be inferred to estimate location every 12 h (Wilson et al. 1992). GLS also recorded saltwater immersion data by testing for saltwater immersion every 30 s, storing the number of samples wet (>0) at the end of each

10 min period. We used saltwater immersion to estimate daily activity budget. Despite the higher mean spatial error of location estimates with these devices (over 100 km; Phillips et al. (2004a)), GLS loggers allowed us to track the birds for prolonged periods with minimal disturbance to them. We considered the following stages regarding the year of GLS deployment (see Table 1): juvenile, as a fledgling equipped with a GLS just before leaving the colony for the first time; immature, as a non-breeding young bird that had never bred equipped with a GLS when visiting the colony; adult, as a breeding adult equipped with a GLS during the incubation or brooding period which successfully fledged a chick and thereafter took a sabbatical year. To date, we have retrieved 40 of the 50 GLS loggers deployed in total over 4 years, from which 33 individual tracks were estimated (Table 2). Our original aim was to collect activity data over the three life-stages on a long period of time (>1 year). These data are available from a total of 10 adults tracked throughout their sabbatical period, 13 immature birds and 10 juvenile birds (up to 3.2 years).

Data processing

The raw immersion data were obtained from testing saltwater immersion every 30 s, the GLS storing the number of samples wet (> 0) at the end of each 10 min period. The data were values from 0 (no immersion or dry, in flight or sitting on the ground) to 200 (permanently immersed in sea water or wet), indicating the number of 3 s periods during 10 min blocks when the sensor was immersed in saltwater. Loggers recorded proportion of time in seawater at 10 min intervals, which we summarized as hours in the water per day (hereafter time spent on water; 10 min blocks immersion data > 0). This measure is a reliable proxy of foraging effort linked to foraging behaviour of the species which enters the water principally to forage (Weimerskirch and Guionnet 2002). Additionally, the duration of the bouts spent entirely immersed (10 min blocks immersion data = 200) was calculated daily (hereafter referred as wet bouts duration). Conversely, when birds are not on land, the time spent dry was interpreted as flying (and thus not feeding). The duration of the bouts spent entirely dry (10 min blocks immersion data = 0) was calculated daily (hereafter referred as dry bouts duration). Additionally the numbers of bouts (number of wet bouts -sitting on water-and of dry bouts -flying) were obtained daily. Although the loggers integrated activity within each 10 min block and so did not provide the exact timing of landings and take-offs, Phalan et al. (2007) found for comparative purposes that bouts defined as a continuous sequence of 0 values for flight (dry) and a sequence of values of 1 or greater for wet bouts, were suitable proxies for activity.

To select the data corresponding to periods spent at sea after leaving the breeding site, we used the following criteria on activity to define the departure time from the colony for each stage: 1) juveniles, the first bout spent on seawater (wet bouts duration) > 1h based on PTT tracking data (Weimerskirch et al. unpublished data); 2) immatures and adults, the last bout spent flying (dry bouts duration) > 12h based on PTT tracking data (Weimerskirch et al. unpublished data). Using these criteria we obtained departure months as follows: 1) the juveniles fledged from the colony from January to March, 2) the immatures left between April and August, and 3) the departures of sabbatical adults were spread over two periods, first between December and February and then from May to July.

Statistical analyses

Variation in activity parameters

The aim was to determine whether distinct foraging behaviours could be detected across the patterns of variation of wet/dry data, and then to appraise how these behaviours varied over time and among individuals. First, to deal with the fact that wet/dry metrics were interrelated (number of wet bouts sitting on water and time spent on water, wet bouts duration and dry bouts duration, wet bouts number and dry bouts number) and to avoid redundancy, we ran principal components analyses (PCA built with the 'PCA' function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe behaviours using gradients of activity we ran PCA for i) all stages (PCS; based on activity data collected during the first ten months post-departure) and for ii) juveniles only, as an additional goal was to determine changes in activity patterns during the first two years of life (PCJ; based on activity data collected during the first twenty-nine months post-departure).

Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance. The first principal component (PC1S) explained 41.5% of the total variance, and correlated positively with time spent on water (r = 0.97) and negatively with dry bouts number (r = -0.79). The second principal component (PC2S) explained 32.5% of the variation and correlated positively with wet bouts duration (r = 0.79) and negatively with wet bouts number (r = -0.75). The third principal component (PC3S) explained 20.2% of the variation and correlated positively with dry bouts duration (r = 0.74) and negatively with dry bouts number (r = -0.44).

Considering juveniles, the first three principal component (PCJ) explained 92.2% of the total variance. The first principal component (PC1J) explained 42.3% of the total variance, and correlated positively with time spent on water (r = 0.98) and negatively with dry bouts number (r = -0.76). The second principal component (PC2J) explained 32.2% of the variation and correlated positively with wet bouts duration (r = 0.72) and negatively with wet bouts number (r = -0.75). The third principal component (PC3J) explained 20.7% of the variation and correlated positively with dry bouts duration (r = 0.48) and negatively with dry bouts number (r = -0.46) and wet bouts duration (r = -0.46).

Second, we used generalized additive mixed models (GAMMs, built with the ‘gam’ function, itsadug and mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with each of the three first axes of the PCA as the dependent variable. We separately ran models testing for variability in activity parameters i) for all stages combined (PCS) and ii) for juveniles (PCJ), based on different duration of datasets (28 months since departure for juveniles and 9 months since departure for immatures and adults; see Supplementary; Table S2). Thus, for i) we considered the lowest number of months elapsed since departure available (9 months since departure). Months elapsed since departure (the duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on), month of the year (i.e. January and so on), sex, and stage (only for i)) were included as fixed effects.. To test for the importance of individual variability in our results we built models with or without random effects. We compared models without random effect, models with random intercepts, and models with random slopes and intercepts to test whether the rate of change of activity parameters as a function of time elapsed since departure varied between individuals (Zuur 2009a). Models included month elapsed since departure as a continuous covariate modelled with non-parametric smoothing functions (Wood 2017). We limited the amount of smoothing (k) with the 'gam.check' function following Wood (2017) for each spline to avoid excessive flexibility and model overfitting that would have no ecological meaning. Models including all combinations of explanatory variables and random effects were then tested and ranked using their Akaike Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach (Burnham and Anderson 2002). The model with the lowest AIC was considered as the best model. Two models separated by a difference in AIC values of less than 2 were assumed to fit the data similarly.

Variation in body size

Differences between sexes in body size measurements were tested using Student's t-tests and Wilcoxon rank tests. We tested independently if each measurements (wing length, tarsus length, bill length, bill depth and body mass) varied according to sex and stage (juvenile and adult). The effects were tested using generalised linear models (GLMs) with a Gaussian family and identity link function (Zuur 2009b). Model validation and model selection were performed following (Zuur 2009b). Although sexes and stages differed for some body size measurements, we could not include body size as an additional explanatory variable in GAMMs testing for factors of variation in activity patterns due to small sample sizes in each sex and stage category, and due to unbalanced sampling.

Spatial and statistical analyses were performed using (R Core Team 2021). Values are means ± SD.

Results

Changes in activity for all stages

The most parsimonious models explaining variations in activity parameters in Amsterdam albatross included time elapsed since departure from the colony, month of the year, stages and sexes (Table 3; Supplementary Figures S1 - S5; Tables S2 and S3), whatever the synthetic activity variables considered (PC1S, PC2S and PC3S). Selected models also included random effects on intercepts and slopes, indicating inter-individual variability in activity and inter-individual variability in the rate of change of activity as a function of time elapsed since departure from the colony.

Compared to adults, immatures and even more so juveniles, spent a lower percentage of time on water (Table 4, Supplementary Figures S1) and made more flying bouts (PC1S; Supplementary Figures S2), made shorter and fewer bouts on water (PC2S; Supplementary Figures S4-S5), and made longer flying bouts (PC3S; Supplementary Figures S2). Males spent a higher percentage of time on water and made fewer flying bouts (PC1S), longer and more numerous bouts on water (PC2S) and shorter flying bouts (PC3S) compared to females. The two synthetic activity variables (PC1S, PC2S) also varied significantly with time exhibiting clear nonlinear temporal patterns (Figure 1). These variations were related to the time elapsed since their departure from the colony and showed seasonal changes (indicated by the month of the year; Supplementary Figures S1 - S5; Tables S2 and S3). With increasing time since departure birds spent lower percentage of time on water and made shorter wet bouts. They spent less percentage of time on water during the period March to July compared to rest of the year (PC1S, Supplementary Figures S1 - S5). They made longer and fewer bouts on water during the period April to November, and shorter flying bouts during the period November to February. Juveniles showed strong and abrupt temporal changes in activity linked to the time elapsed since departure from the colony in the first two months after fledging (Supplementary Figure S6). In immatures and adults the temporal pattern appeared reversed compared to juveniles (Supplementary Figure S6).

Changes in activity of juveniles during the first two years after fledging

In juveniles Amsterdam albatross, the most parsimonious models explaining variations in activity included time elapsed since departure from the colony, month of the year whatever the activity variables considered (Table 5; PC1J, PC2J and PC3J), and sexes (PC2J and PC3J). Selected models also included random effects on intercepts and slopes, indicating inter-individual variability in activity and inter-individual variability in the rate of change of activity as a function of time elapsed since departure from the colony (Supplementary Figures S7).

PC2J and PC3J varied significantly with sex (Supplementary Figures S8 - S11; Tables S5b, 5c), indicating that juvenile males made shorter and more numerous bouts on water (PC2J) and shorter flying bouts (PC3J) compared to females (Supplementary Figures S8 - S11; Tables S5b, 5c). PC1J and PC2J varied significantly with time exhibiting clear nonlinear temporal patterns (Figure 2; Supplementary Figures S8 - S12; Tables S2 and S4a, 4b). Juveniles seemed to alternate periods of lower percentage of time spent on water combined with more numerous flying bouts (April) with periods of higher percentage of time on water combined with fewer flying bouts (February, July-October; PC1J, not illustrated). The seasonal change was also observed through longer and fewer bouts spent on water and shorter flying bouts at the end of the year (PC2J: September-December). Juveniles, during the first 28 months after fledging, increased the time spent on water while decreasing the number of flying bouts (Figure 2a).

Body size

Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and bill depth whatever the stage (juvenile or adult; Tables 6-12). In juveniles, males were ~13% heavier than females, while the difference was not significant in adults (Table 6). The most sexually dimorphic phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they were body mass, tarsus length and bill length.

Discussion

Using miniaturized activity loggers (GLS), we showed clear differences and changes in activity characteristics depending on life-stages, time and sex. By comparing changes in behaviour at sea and foraging parameters of juveniles after their departure at sea with those of immatures and adults in the Amsterdam albatross, we showed that juveniles differed from immatures and adults in their activity values and patterns. In this study, we benefited from a unique comprehensive dataset of remarkable duration (up to 28 months) to characterise the post-fledging behaviour of naïve seabirds. Although one limitation of our study was that individual longitudinal data were not long enough to explore changes in behaviour from fledging to the adult stage, these results provide new insights into the timing and the change of behaviour in naïve individuals over a unique dataset in a long-lived endangered seabird species.

Stage specific changes

The birds were found to behave differently according to their stage whatever the activity variables considered, indicating differences in foraging behaviour. Overall, juveniles spent lower percentage of time on water compared to immatures and adults. Nonetheless, during the first month following their departure from the colony while the proportion of time spent on water by immatures and adults showed a dome-shaped curve peaking three to five months after departure, juveniles changed abruptly, with values dropping off in the first two months and then remaining low and overall lower than in adults and immatures. This might indicate a lower foraging activity in naïve birds. During the same period, the duration and number of water bouts also exhibited progressive change. These patterns suggest an early and gradual change in foraging behaviour and that juveniles progressively behaved similarly to immatures and adults (reaching similar values in activity covariates). It is noteworthy that the multi-monthly bell-shaped pattern observed during the first 10 months after departure in immatures and adults appears to be mirrored in juveniles 15-16 months later (see Figure S12). Together, these results suggest a progressive behavioural change in movements during the first two months after fledging. This seems to indicate that juvenile individuals may have weaker foraging skills during their first two months at sea. Although behavioural changes can often equate to improved performance (e.g. Campioni et al. 2020) this is not always the case. The emergence of juvenile birds as more '*adult like*' in their foraging/flight behavioural patterns is not necessarily a sign of improvement.

Results suggest that immatures may differ from both adults and juveniles in some aspects of their behaviour. While most of the activity parameters and the temporal patterns showed similarities with adults when considering the time elapsed since departure, they seemed rather comparable to juveniles when considering seasonal aspects (month of the year). Such inconsistency can be explained by several non-exclusive explanations: i) similar management of energy constraints than adults, as post-breeding adults and immatures are less constrained in their central-place foraging strategies (Campioni et al. 2016), ii) comparable capacity to respond to local resource availability in their foraging behaviour than juveniles (Frankish et al. 2022), and iii) incomplete acquisition of more long-term learning of complex movement strategies (Thorup et al. 2003; Votier et al. 2011; Rotics et al. 2016). Disentangling among these hypotheses can be achieved by combining higher resolution movement data with longer longitudinal studies covering all three life stages for same individuals.

Since all stages of the Amsterdam albatross forage in the same water masses (see Thiebot et al. 2014), differences in foraging behaviour were presumably not due to different oceanographic characteristics as observed in other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al. 2020b). These lower performances could be due to a combination of lack of experience of optimal behaviours, poor knowledge of the environment, use of distinct cues and/or physical immaturity (Shaffer et al. 2001; Frankish et al. 2020a, 2022). It is likely that increasing exposure to diverse foraging situations allows juveniles to rapidly accumulate foraging experience and improve various aspects of foraging.

What might be designated as '*lower performance*' of juveniles found in our study is consistent with studies on wandering albatrosses and Amsterdam albatrosses (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2017; Pajot et al. 2021) during the first weeks at sea. Fledging juvenile albatrosses behaved differently and that shortly after they employ similar foraging strategies as adults (Frankish et al. 2022). Additional skills (such as detection of prey at the surface, detection of other foraging seabirds, navigational skills…) need to be acquired during the immature period before the efficiency of these behaviors matches that of adults. This is also typical of other seabird taxa, which show progressive improvement in flight performance with the numbers of days since fledging (Yoda et al. 2004; Mendez et al. 2017; Collet et al. 2020; Corbeau et al. 2020; Frankish et al. 2022). For example juvenile brown boobies *Anous stolidus* improved their flight abilities (Yoda et al. 2004) and juvenile European shags *Phalacrocorax aristotelis* compensate for poor foraging success by increasing their foraging time during first months after fledging (Daunt et al. 2007). In contrast, flight capability (flight speed and sinuosity) comparable to that of adults allows juvenile white-chinned petrels *Procellaria aequinoctialis* to rapidly flew large distances from the colony (Frankish et al. 2020).

Notwithstanding the progressive change of movement behaviours (foraging parameters estimated from activity parameters improved with time elapsed) quantified in juvenile Amsterdam albatrosses, it remains elusive whether this is a question of physical development and/or a matter of gaining experience. Elucidating the transition to independence in early life stages is crucial for understanding the causes of higher juvenile mortality in long-lived species (Fay et al. 2015; Payo-Payo et al. 2016).

Temporal changes in activity

The temporal variability of activity was found whatever the life-stage considered. Part of the activity changes observed following the departure of juveniles Amsterdam albatross may illustrate the swift change in travel and movement behaviour, reflecting a more '*adult like*' behaving, not indicating necessarily an improvement of flight performances and of the ability to cope with changing (i.e. increasing wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such as albatrosses. Both extrinsic (i.e. environmental conditions: variability in subtropical waters resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew) factors could be involved in the modulation of foraging behaviour, which can be reflected in the temporal variability. Subtropical environments in the southern Indian Ocean are generally characterized as oligotrophic areas but nonetheless are known to vary over the seasons. During the austral winter, colder surface waters and strong winds result in changes of oceanographic conditions associated with an increased primary productivity (Behera and Yamagata 2001; Terray 2011; Delord et al. 2021). Changes in water temperature associated with wind appear to result in seasonal biological production variations that affect seabirds (Delord et al. 2021).

In seabirds, temporal changes in foraging activities are often associated to the very strong contrast between reproduction and inter-breeding periods, shifting from high energetic needs linked to reproductive effort and associated constraints (i.e. central place foraging strategy; Orians and Pearson 1979) to a reduction of these energetic constraints during the non-breeding period (sabbatical year for adults) (Williams 1966; Ricklefs 1977, 1983; Stearns 1992; Ydenberg et al. 1992). This contrast is particularly pronounced in seabirds (Mackley et al. 2010; Gutowsky et al. 2014) where energetic constraints play a decisive role in determining activity patterns (Phalan et al. 2007).

Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting important constraints (Weimerskirch 1991; see Supplementary). Recently Gutowsky et al. (2014) suggested that tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could compromise flight from active wing moult during the non-breeding period and induce changes in daily activity budget during a 'quasi-flightless' stage. However, there is no such data for southern albatrosses. Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested it such a compromise. However, adult birds during the non-breeding season appear to spend much more time on the water during winter, suggesting that partial moult may occur at this time, as observed in many other seabird species that have to moult during the non-breeding season and show reduced activity during specific periods that may correspond to moulting (Weimerskirch et al. 2015b, 2020). Interestingly, immature appear to have this peak in time spent on the water in spring, suggesting different timing of moult.

Sex differences in activity

Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013; Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by differences in foraging habitats. We found support for the body-size hypothesis to explain sex differences in activity parameters, consistent with the important sexual dimorphism in the Amsterdam albatross. Males did more bouts on water whatever the stage, and depending on stage, shorter (juveniles only) compared to females. Consistently, we found that males flew for longer periods (dry bouts duration) compared to females. When considering all stages, males spent a higher percentage of time on water compared to females.

Amsterdam albatross and its sister species the wandering albatross have a very close anatomy and similar use of the wind, although Amsterdam albatross is 5-8% smaller and 25% lighter (Barbraud et al. unpublished data. In the wandering albatross, due to sex differences in flight performance (specifically, due to their higher wing loading), males should both maintain longer flying effort and be more likely to minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). The change in foraging strategy, as in wandering albatross, tends to be dependent on breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a greater use of the '*sit-and-wait*' technique and may vary between sites, suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the '*sit-and-wait*' technique (compared to '*foraging-in-flight*'). In other word, males may have more of a '*sit-and-wait*' strategy while females have more of a '*foraging-in-flight*' strategy, although there is some behavioural plasticity particularly over time. Our prediction that foraging behaviour differs between sexes was fully supported (i.e. sex-differences in activity parameters). Nevertheless, the similarity in time spent on the water suggests that the differences may be more subtle, showing some a trade-offs in duration and numbers between flying and water bouts. This trade-off should vary depending on stage as immature females tended to have shorter and more frequent bouts on the water. This implies that while probably feeding on similar water masses, the sexes might differ in type of prey targeted and/or used different foraging methods. The confirmation of this hypothesis reinforces the fact that the two-sibling species, as previously assumed, show a high degree of similarity in their foraging behaviour.

Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey (Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019; Barbraud et al. 2021). It has also been suggested that size matters probably because the smaller and lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower wing loaded female wandering albatrosses, compared to males, are probably better able to exploit subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al. (2002); Stauss et al. (2012)).

Individual variability in activity

There was inter-individual variability in almost all activity parameters whatever the stage considered. In juveniles, models indicated inter-individual variability in activity and in the rate of change of activity as a function of time elapsed since departure from the colony. Since the intercept terms in the models were significant, it seems as though individual variability (i.e., specialization on different foraging strategies) was a contributor to observed variability. However, the rate of change of intra-individual variation for some foraging strategies (percentage of time on water-number of flying bouts axis) oscillated during the juvenile period with a seemingly remarkable synchrony (see Fig S7). This suggests that changes in foraging behaviours occurred at the individual level during the juvenile period without stabilizing, at least during the first two years after fledging. This individual variability suggests development of specialized individual foraging behaviours (Harel et al. 2016; Rotics et al. 2016, 2021; Phillips et al. 2017). Nonetheless, given the small sample sizes these results should be interpreted with caution.

Conclusion

Very few studies have investigated the ontogeny of foraging behaviour over such a long period of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over several years. We investigated the foraging behaviour, through activity patterns, during the three life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naïve juveniles, immatures and adults. Naïve juveniles during their first month at sea after leaving their colony exhibited lower foraging activity (greater proportion of time spent sitting on water, longer and more numerous bouts on water, and shorter and fewer flying bouts). Patterns of activity parameters in juveniles after independence suggested a progressive change of foraging performances during the first two months since fledging. Regardless of life stage considered, activity parameters exhibited temporal variability reflecting the modulation of foraging behaviour presumably linked to both extrinsic (i.e. environmental conditions such as variability in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew during moult) factors. Sex differences in activity parameters according to time since departure from the colony and season were consistent with the sexual dimorphism in the Amsterdam albatross. It is therefore expected that a change in behaviour, resulting from the experience gained, may reflect an improvement in skills occurring during a period of learning through the immaturity phase.

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Table 1 Chronological characteristics of life-cycle stages of Amsterdam albatross (adapted from Thiebot et al. 2014)

Stage[1]	Definition	Age[1]	Tracking duration	Behaviour
Juvenile	Following chick fledging in January	1st year	~2.5 years	Chicks disperse at sea after leaving the colony for the first time
Immature	After juvenile dispersal, until first breeding attempt (at 9 year old on average)	~2-10 years	~1 year	Non-breeding young birds forage at sea and occasionally visit the colony for mating
Adult sabbatical	Between two successive breeding periods (~ 15 January year t to the following 15 January year $t+1$)	~8-28 years	~1 year	Breeding adults at the end of reproductive cycle and leave the colony to forage at sea

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[1] Stage/Age at which the individuals were equipped with loggers in our study

Table 2 Sample sizes of birds tracked using Global Location Sensing (GLS) of Amsterdam albatross

Stage	Years of deployment	Deployed (n)	Recovered (n)	Recovery rate (%)	GLS with data (n)
Juvenile	2011	21	12	57 (t+9)	10 (4 F - 6 M)[1]
Immature	2011-2012	18	17	94	13 (3 F - 9 M – 1 NK)
Adult sabbatical	2006, 2009	11	11	100	10 (6 F - 4 M)

[1] number of females F and males M, or not known NK for each stage

Table 3 Model selection for variations in activity parameters of Amsterdam albatrosses in relation to sex, stage, number of months spent since departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on)

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1S)				
M_0	Null model		28874.42	0
M_1	Month elapsed	Month elapsed: Individual	27311.97	1562.45
M_2	Month elapsed + Month	Month elapsed: Individual	26968.28	1906.14
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	26889.23	1985.19
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	26852.86	2021.56
Bouts spent on water (PC2S)				
M_0	Null model		26903.12	0
M_1	Month elapsed	Month elapsed: Individual	25803.80	1099.32
M_2	Month elapsed + Month	Month elapsed: Individual	25756.37	1146.75
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	25751.47	1151.65
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	25752.62	1150.50
Bouts spent dry -flying (PC3S)				
M_0	Null model		23042.26	0

M_1	Null model	Month elapsed: Individual	22540.25	502.01
M_2	Month elapsed	Month elapsed: Individual	22539.75	502.51
M_3	Month	Month elapsed: Individual	22509.79	532.47
M_4	Month + Stage + Sex	Month elapsed: Individual	22427.29	614.97

Models are ranked according to decreasing statistical support, as indicated by AICc. The first best models are shown

Table 4 Values of activity parameters (mean ± sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam albatross

	Juvenile[1]		Juvenile[2]		Immature		Adult sabbatical	
	female	male	female	male	female	male	female	male
Time spent on water (%)	55.04 ± 20.46	58.18 ± 21.11	51.41 ± 19.18	52.88 ± 20.39	59.25 ± 21.53	63.31 ± 21.17	64.89 ± 20.90	69.98 ± 18.10
Wet bouts (sitting on water) duration (h)	1.21 ± 1.74	1.24 ± 1.76	1.16 ± 1.73	1.12 ± 1.59	1.07 ± 1.31	1.48 ± 2.12	1.47 ± 1.95	1.33 ± 1.96
Dry bouts duration (h)	1.29 ± 1.37	1.21 ± 1.32	1.34 ± 1.41	1.26 ± 1.40	1.32 ± 1.42	1.28 ± 1.55	1.44 ± 1.56	1.31 ± 1.42
Wet bouts (sitting on water) number	8.71 ± 4.01	8.76 ± 4.09	8.14 ± 3.85	8.48 ± 4.11	10.34 ± 4.29	8.59 ± 4.24	8.96 ± 3.98	10.28 ± 5.33
Dry bouts number	7.06 ± 3.20	7.27 ± 3.52	7.57 ± 3.21	7.85 ± 3.50	6.31 ± 3.21	5.75 ± 2.99	5.01 ± 2.64	4.64 ± 2.48

[1] calculated during 28 months following departure; [2] calculated during 9 months following departure

Table 5 Model selection for variations activity parameters for juveniles Amsterdam albatrosses in relation to sex, number of months spent since departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on)

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1J)				
M_0	Null model		22109.52	0
M_1	Month elapsed	Month elapsed: Individual	21864.11	245.41
M_2	Month elapsed + Month	Month elapsed: Individual	21625.69	483.83
Bouts spent on water (PC2J)				
M_0	Null model		20417.76	0
M_1	Month elapsed	Month elapsed: Individual	20072.42	345.34
M_2	Month elapsed + Month	Month elapsed: Individual	20004.65	413.11
M_3	Month elapsed + Month + Sex	Month elapsed: Individual	19999.00	418.76
Bouts spent dry -flying (PC3J)				
M_0	Null model		17708.47	0
M_1	Null model	Month elapsed: Individual	17548.75	159.72
M_2	Month elapsed	Month elapsed: Individual	17549.00	159.47
M_3	Month + Sex	Month elapsed: Individual	17541.02	167.45

Models are ranked according to decreasing statistical support, as indicated by AICc. The first best models are shown

Table 6 Body measurements of juveniles and adults Amsterdam albatross and percentage of differences between sexes for each measurement. Δ is the difference in %, p values are reported

	Juvenile		Adult		Δ		Dimorphism ratio[1]		t-test[2]	
	Female (n=159)	Male (n=162)	Female (n=30)	Male (n=45)	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
Wing length (mm)	532.3 ± 62.1	543.6 ± 72.5	637.0 ± 13.3	654.7 ± 14.7	2.1	2.7	1.021	1.026	**W=10554** **P<0.01**	**t_{64}=-4.882** **p<0.001**
Tarsus length (mm)	113.1 ± 3.8	118.4 ± 3.8	112.4 ± 3.9	116.4 ± 4.0	4.5	3.5	1.047	1.077	**t_{229}= -10.54** **p<0.001**	**t_{28}= -3.982** **p<0.001**
Bill length (mm)	137.1 ± 4.0	143.1 ± 3.8	140.9 ± 4.7	145.0 ± 3.5	4.2	2.8	1.044	1.034	**t_{319}= -13.89** **p<0.001**	**t_{72}= -4.268** **p<0.001**
Bill depth (mm)	34.8 ± 3.4	36.9 ± 3.4	36.0 ± 1.5	38.0 ± 1.5	5.8	5.2	1.061	1.000	**t_{318}= -5.629** **p<0.001**	**t_{58}= -4.821** **p<0.001**
Body mass (g)	7719 ± 1228	8859 ± 1546	7509 ± 1561	7257 ± 1207	12.9	3.4	1.148	1.077	**t_{193}=-5.846** **p<0.001**	t_{32}=0.512 p=0.612

[1] ratio calculated as Male/Female following (Lovich and Gibbons 1992) for species for which males are known to be larger than females cited in (Smith 1999); [2] Student's t-tests used after check for normality of the data for all measurements except for wing length of juveniles (Wilcoxon rank test)

Table 7 Selected generalized linear models testing for the effect of sex and stage on body measurements of Amsterdam albatross

Model #	**Study variable**	**Model**	**Sample size**
GLM1	Wing length	~ sex + stage	387
GLM2	Tarsus length	~ sex + stage	299
GLM3	Bill length	~ sex	395
GLM4	Bill depth	~ sex	380
GLM5	Body mass	~ sex + stage	242

Table 8 GLM results for wing length of Amsterdam albatross modelled as a function of sex and stage (GML1). Reference values are female and adult. The degrees of freedom were 384

	Estimate	Std.Error	t-value	p-value
(Intercept)	638,68	17,43	36,651	p<0.001
Male	16,97	7,28	2,331	p<0.05
Juvenile	-95,24	17,27	-5,516	p<0.001

Table 9 GLM results for tarsus length of Amsterdam albatross modelled as a function of sex and stage (GLM2). Reference values are female and adult. The degrees of freedom were 296

	Estimate	Std.Error	t-value	p-value
(Intercept)	110,54	0,95	116,42	p<0.001
Male	4,92	0,45	11,01	p<0.001
Juvenile	2,56	0,94	2,73	p<0.01

Table 10 GLM results for bill length of Amsterdam albatross modelled as a function of sex (GLM3). Reference values are female. The degrees of freedom were 393

	Estimate	Std.Error	t-value	p-value
(Intercept)	137,65	0,30	462,98	p<0.001
Male	5,88	0,41	14,31	p<0.001

Table 11 GLM results for bill depth of Amsterdam albatross modelled as a function of sex (GLM4). Reference values are female. The degrees of freedom were 378

	Estimate	Std.Error	t-value	p-value
(Intercept)	34,94	0,24	147,74	p<0.001
Male	2,16	0,33	6,60	p<0.001

Table 12 GLM results for body mass of Amsterdam albatross modelled as a function of sex and stage (GLM5). Reference values are female and adult. The degrees of freedom were 239

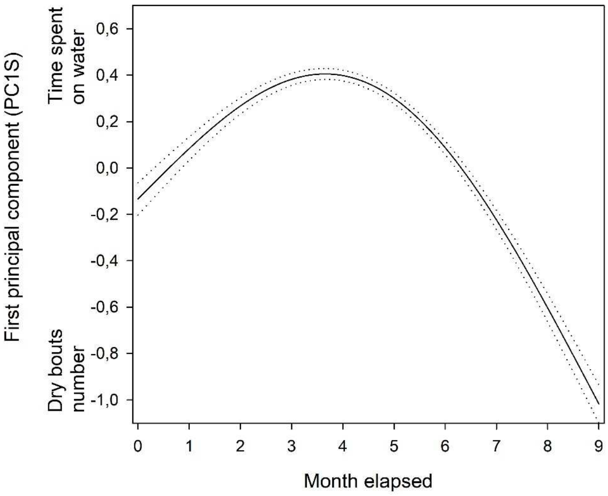
	Estimate	Std.Error	t-value	p-value
(Intercept)	6777,60	417,10	16,25	p<0.001
Male	911,50	186,20	4,90	p<0.001
Juvenile	958,70	412,80	2,32	p<0.01

FIGURES

Figure 1 Modeled a) first and b) second axis of principal components analysis of activity parameters of all stages (i.e. adult, immature and juvenile) of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval.

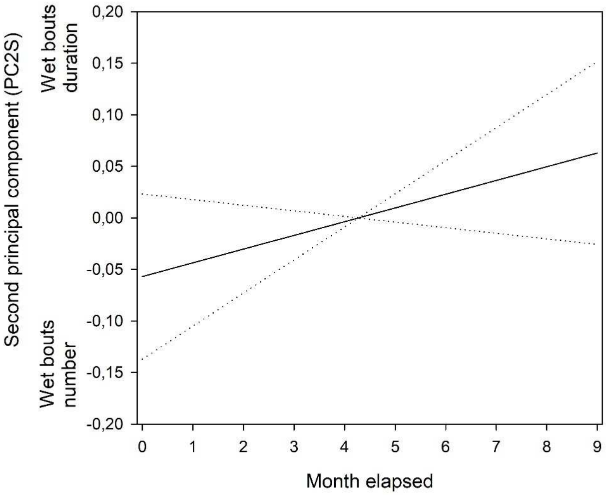
Figure 2 Modeled a) first and b) second axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval.

1167 Figure 1a



1168

1169 Figure 1b



1170

Figure 2a

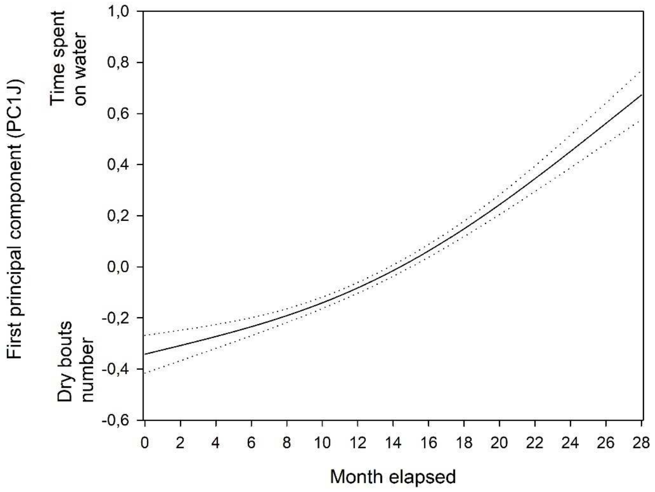
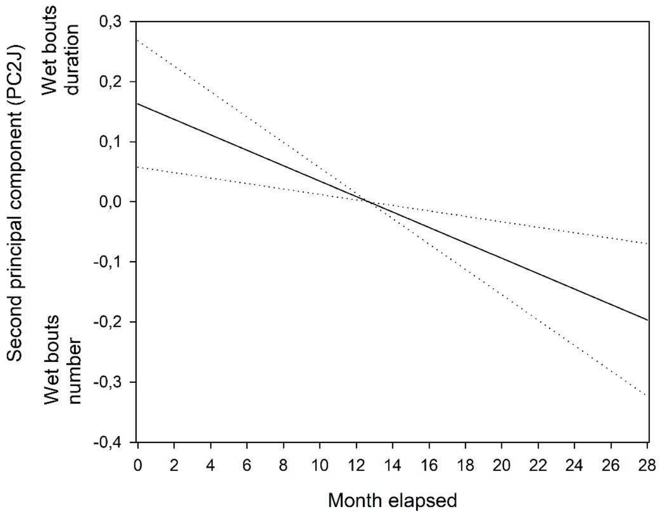


Figure 2b



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REFERENCES

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Bird migration. Springer, pp 331–351

Austin RE, De Pascalis F, Arnould JP, et al (2019) A sex-influenced flexible foraging strategy in a tropical seabird, the magnificent frigatebird. Marine Ecology Progress Series 611:203–214

Barbraud C, Delord K, Kato A, et al (2021) Sexual segregation in a highly pagophilic and sexually dimorphic marine predator. Peer Community Journal 1:e71. DOI: 10.24072/pcjournal.75. bioRxiv 472431

Becker J (2014) Dispersal and Genetic Variation in a Naturally Fragmented Environment: Insights from a Long-term Study of White-throated Dippers (Cinclus cinclus). Doctoral dissertation, University of Zurich. https://www.zora.uzh.ch/id/eprint/102335/1/BeckerPhilipp_PhD-thesis_2014.pdf. Accessed on 29/07/2022

Behera SK, Yamagata T (2001) Subtropical SST dipole events in the southern Indian Ocean. Geophysical Research Letters 28:327–330

Belkin, IM, Gordon, AL (1996) Southern Ocean fronts from the Greenwich meridian to Tasmania. Journal of Geophysical Research: Oceans, 101(C2), 3675-3696

Boynton CK, Mahony NA, Williams TD (2020) Barn Swallow (Hirundo rustica) fledglings use crop habitat more frequently in relation to its availability than pasture and other habitat types. The Condor 122:duz067

Bruner JS (1972) Nature and uses of immaturity. American psychologist 27:687

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. NewYork,NY.

Burns JM, Clark CA, Richmond JP (2004) The impact of lactation strategy on physiological development of juvenile marine mammals: implications for the transition to independent foraging. Elsevier, pp 341–350

Campioni L, Dias MP, Granadeiro JP, Catry P (2020) An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. Journal of Animal Ecology 89:29–43

Campioni L, Granadeiro JP, Catry P (2016) Niche segregation between immature and adult seabirds: does progressive maturation play a role? Behavioral Ecology 27:426–433

Caubet Y, Jaisson P, Lenoir A (1992) Preimaginal induction of adult behaviour in insects. The Quarterly Journal of Experimental Psychology Section B 44:165–178

Clay TA, Joo R, Weimerskirch H, et al (2020) Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. Journal of Animal Ecology 89:1811–1823

Collet J, Prudor A, Corbeau A, et al (2020) First explorations: ontogeny of central place foraging directions in two tropical seabirds. Behavioral Ecology 31:815–825

Corbeau A, Prudor A, Kato A, Weimerskirch H (2020b) Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. Journal of Animal Ecology 89:20–28. https://doi.org/10.1111/1365-2656.13121

Daunt F, Afanasyev V, Adam A, et al (2007) From cradle to early grave: juvenile mortality in European shags Phalacrocorax aristotelis results from inadequate development of foraging proficiency. Biology Letters 3:371–374. https://doi.org/10.1098/rsbl.2007.0157

de Grissac S, Bartumeus F, Cox SL, Weimerskirch H (2017) Early-life foraging: Behavioral responses of newly fledged albatrosses to environmental conditions. Ecology and evolution 7:6766–6778

de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. Scientific reports 6:26103

Delord K, Barbraud C, Bost CA, et al (2013) Atlas of top predators from the French Southern Territories in the Southern Indian Ocean. http://www.cebc.cnrs.fr/ecomm/Fr_ecomm/ecomm_ecor_OI1.html

Delord K, Cotté C, Terray P, et al (2021) Factors affecting adult body condition in the endangered northern rockhopper penguin. Marine Biology 168:1–15

Dukas R (2006) Learning in the context of sexual behaviour in insects. Animal Biology 56:125–141

Ellis HI, Gabrielsen GW (2002) Energetics of free-ranging seabirds. In: Seabirds energetics, Whittow, G. C. and Rahn, H. Plenum Press, N.Y., pp 359–408

Evans DR (2018) The post-fledging survival and movements of juvenile Barn Swallows (Hirundo rustica): an automated telemetry approach. Electronic Thesis and Dissertation Repository. 5791. https://ir.lib.uwo.ca/etd/5791. Accessed on 29/07/2022

Fay R, Weimerskirch H, Delord K, Barbraud C (2015) Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. Journal of Animal Ecology 84:1423–1433

Frankish CK, Manica A, Clay TA, et al (2022) Ontogeny of movement patterns and habitat selection in juvenile albatrosses. Oikos e09057

Frankish CK, Manica A, Phillips RA (2020a) Effects of age on foraging behavior in two closely related albatross species. Movement ecology 8:7

Frankish CK, Phillips RA, Clay TA, et al (2020b) Environmental drivers of movement in a threatened seabird: insights from a mechanistic model and implications for conservation. Diversity and Distributions 26:1315–1329

Furness RW (1988) Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed albatross Diomedea chlororhynchos. J Zool 215:719–727

Gonzales-Solis J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels Macronectes halli during incubation. Oikos 90:390–398

Gutowsky SE, Gutowsky LF, Jonsen ID, et al (2014) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. Movement ecology 2:23–23

Harel R, Horvitz N, Nathan R (2016) Adult vultures outperform juveniles in challenging thermal soaring conditions. Scientific reports 6:27865. https://doi.org/10.1038/srep27865

Heyes CM (1994) Social learning in animals: categories and mechanisms. Biological Reviews 69:207–231

Jaeger A, Jaquemet S, Phillips RA, et al (2013) Stable isotopes document inter- and intra-specific variation in feeding ecology of nine large southern Procellariiformes. Mar Ecol Prog Ser 490:255–266

Jouventin P, Martinez J, Roux J-P (1989) Breeding biology and current status of the Amsterdam Island Albatross *Diomedea amsterdamensis*. Ibis 131(2):171-182

King JR (1974) Seasonal allocation of time and energy resources in birds. Avian energetics 4–85

Krüger S, Reid T, Amar A (2014) Differential range use between age classes of southern African Bearded Vultures Gypaetus barbatus. PLoS One 9(12), e114920. DOI: 10.1371/journal.pone.0114920

Lack D (1954) The natural regulation of animal numbers. The Natural Regulation of Animal Numbers

Langen TA (1996) Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, Calocitta formosa. Animal Behaviour 51:575–588

Langston NE, Rohwer S (1996) Molt-breeding tradeoffs in albatrosses : life history implications for big birds. Oikos 76:498–510

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. Journal of statistical software 25:1–18

Lewis S, Benvenuti S, Dall–Antonia L, et al (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proceedings of the Royal Society of London Series B: Biological Sciences 269:1687–1693

Lin X, Zhang D (1999) Inference in generalized additive mixed modelsby using smoothing splines. Journal of the royal statistical society: Series b (statistical methodology) 61:381–400

Louzao M, Wiegand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Movement ecology 2:1–15

Lovich JE, Gibbons JW (1992) A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging 56:269–269

Mackley EK, Phillips RA, Silk JR, et al (2010) Free as a bird? Activity patterns of albatrosses during the nonbreeding period. Marine Ecology Progress Series 406:291–303

Marchetti K, Price T (1989) Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biological Reviews 64:51–70

Margrath R, Lill A (1985) Age-related differences in behaviour and ecology of crimson rosellas, Platycercus elegans, during the non-breeding season. Wildlife Research 12:299–306

Martin P, Bateson P (1985) The ontogeny of locomotor play behaviour in the domestic cat. Animal behaviour 33:502–510

Mendez L, Prudor A, Weimerskirch H (2017) Ontogeny of foraging behaviour in juvenile red-footed boobies (Sula sula). Scientific reports 7:1–11

Murphy ME (1996) Energetics and nutrition of molt. In: Avian energetics and nutritional ecology. Springer, pp 158–198

Mushinsky HR, Hebrard JJ, Vodopich DS (1982) Ontogeny of water snake foraging ecology. Ecology 63:1624–1629

Naef-Daenzer B, Grüebler MU (2008) Post-fledging range use of Great Tit Parus major families in relation to chick body condition. Ardea 96:181–190

Nevitt GA, Losekoot M, Weimerskirch H (2008) Evidence for olfactory search in wandering albatross, Diomedea exulans. Proceedings of the National Academy of Sciences 105:4576–4581

Nourani E, Vansteelant WMG, Byholm P, Safi K (2020) Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. Biology Letters 16:20190797. https://doi.org/10.1098/rsbl.2019.0797

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of Ecological Systems, Ohio State University Press. Columbus, pp 154–177

Pajot A, Corbeau A, Jambon A, Weimerskirch H (2021) Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. Journal of Avian Biology 52: e02597. https://doi.org/10.1111/jav.02597

Payo-Payo A, Genovart M, Bertolero A, et al (2016) Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. Proceedings of the Royal Society B: Biological Sciences 283:20153042

Peery MZ, Henkel LA, Newman SH, et al (2008) Effects of rapid flight-feather molt on postbreeding dispersal in a pursuit-diving seabird. The Auk 125:113–123

Pennycuick CJ (1982) The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Phil Trans R Soc Lond 300:75–106

Péron C, Grémillet D (2013) Tracking through Life Stages: Adult, Immature and Juvenile Autumn Migration in a Long-Lived Seabird. Plos One 8:e72713

Phalan B, Phillips RA, Silk JR, et al (2007) Foraging behaviour of four albatross species by night and day. Marine Ecology Progress Series 340:271–286

Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Marine Ecology Progress Series 578:117–150

Phillips RA, Mcgill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Marine Biology 158:2199–2208

Phillips RA, Silk JRD, Croxall JP, et al (2004a) Accuracy of geolocation estimates for flying seabirds. Marine Ecology-Progress Series 266:265–272

Phillips RA, Silk JRD, Phalan B, et al (2004b) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proceedings of the Royal Society of LondonSeries B: Biological Sciences 271:1283–1291

Rapaport LG, Brown GR (2008) Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews 17:189–201

Ricklefs RE (1977) On the evolution of reproductive strategies in birds: reproductive effort. American naturalist 111:453–478

Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. Studies of Avian biology 8:84–94

Riotte-Lambert L, Weimerskirch H (2013) Do naive juvenile seabirds forage differently from adults? Proceedings of the Royal Society B: Biological Sciences 280:20131434

Rivalan P, Barbraud C, Inchausti P, Weimerskirch H (2010) Combined impact of longline fisheries and climate on the persistence of the Amsterdam albatross. Ibis 152:6–18

Rotics S, Kaatz M, Resheff YS, et al (2016a) The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. Journal of Animal Ecology 85:938–947

Rotics S, Turjeman S, Kaatz M, et al (2021) Early-life behaviour predicts first-year survival in a long-distance avian migrant. Proceedings of the Royal Society B 288:20202670

Roux JP, Jouventin P, Mougin JL, et al (1983) Un nouvel albatros Diomedea amsterdamensis n. sp. découvert sur l'île Amsterdam (37°50'S, 77°35'E). L'Oiseau et R F O 53:1–11

Ruaux G, Lumineau S, de Margerie E (2020) The development of flight behaviours in birds. Proceedings of the Royal Society B 287:20200668

Sergio F, Tanferna A, De Stephanis R, et al (2014) Individual improvements and selective mortality shape lifelong migratory performance. Nature 515:410–413

Shaffer SA, Weimerskirch H, Costa D (2001) Functional significance of sexual dimorphism in wandering albatrosses, Diomedea exulans. Functional Ecology 15:203–210

Smith RJ (1999) Statistics of sexual size dimorphism. Journal of Human Evolution 36:423–458. https://doi.org/10.1006/jhev.1998.0281

Stauss C, Bearhop S, Bodey T, et al (2012) Sex-specific foraging behaviour in northern gannets Morus bassanus: incidence and implications. Marine Ecology Progress Series 457:151–162

Stearns SC (1992) The Evolution of Life Histories, Oxford: Oxford University Press.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. Accessed 29/07/2022

Terray P (2011) Southern Hemisphere extra-tropical forcing: a new paradigm for El Niño-Southern Oscillation. Climate dynamics 36:2171–2199

Thiebot J-B, Delord K, Marteau C, Weimerskirch H (2014) Stage-dependent distribution of the critically endangered Amsterdam albatross in relation to Economic Exclusive Zones. Endangered Species Research 23:263–276

Thiers L, Delord K, Barbraud C, et al (2014) Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. Mar Ecol Prog Ser 499:233–248

Thorup K, Alerstam T, Hake M, Kjellén N (2003) Bird orientation: compensation for wind drift in migrating raptors is age dependent. Proceedings of the Royal Society of London Series B: Biological Sciences 270:S8–S11

Urios V, López-López P, Limiñana R, Godino A (2010) Ranging behaviour of a juvenile Bearded Vulture (Gypaetus barbatus meridionalis) in South Africa revealed by GPS satellite telemetry. Ornis Fennica, 87(3), 114

Votier SC, Grecian WJ, Patrick S, Newton J (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Marine biology 158:355–362

Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Advances in marine biology 54:107–170

Weimerskirch H (1991) Sex-specific differences in molt strategy in relation to breeding in the wandering albatross. Condor 93:731–737

Weimerskirch H, Akesson S, Pinaud D (2006) Postnatal dispersal of wandering albatrosses *Diomedea exulans*: implications for the conservation of the species. J Avian Biol 37:23–28

Weimerskirch H, Brothers N, Jouventin P (1997a) Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationship with long-line fisheries: conservation implications. Biological conservation 79:257–270

Weimerskirch H, Cherel Y, Delord K, et al (2014) Lifetime foraging patterns of the wandering albatross: Life on the move! Journal of Experimental Marine Biology and Ecology 450:68–78

Weimerskirch H, de Grissac S, Ravache A, et al (2020) At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. Marine Ecology Progress Series 633:225–238

Weimerskirch H, Delord K, Guitteaud A, et al (2015a) Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Scientific Reports 5:8853-

Weimerskirch H, Guionnet T (2002) Comparative activity pattern during foraging of four albatross species. Ibis 144:40–50

Weimerskirch H, Shaffer SA, Tremblay Y, et al (2009) Species-and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Marine Ecology Progress Series 391:267–278

Weimerskirch H, Tarroux A, Chastel O, et al (2015b) Population-specific wintering distributions of adult south polar skuas over the three oceans. Mar Ecol Prog Ser 538:229–237

Weimerskirch H, Wilson RP, Lys P (1997b) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Marine Ecology Progress Series 151:245–254

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack’s principle. American naturalist 687–690

Wilson RP, Ducamp JJ, Rees G, et al (1992) Estimation of location: global coverage using light intensity. In: Priede IMSS (ed). Ellis Horward, Chichester, pp 131–134

Wood S (2015) Package ‘mgcv.’ R package version 1:729

Wood S (2017) Generalized Additive Models: An Introduction with R, 2nd Edition Chapman and Hall//CRC, Boca Raton. Chapman and Hall/CRC

Wynn J, Padget O, Mouritsen H, et al (2020) Natal imprinting to the Earth’s magnetic field in a pelagic seabird. Current Biology 30:2869–2873

Ydenberg RC (1989) Growth-mortality trade-offs and the evolution of juvenile life histories in the alcidae. Ecology 70:1494–1506

Ydenberg RC, Welham CVJ, Schmid-Hempel R, et al (1992) Time and energy constraints and the relationships between currencies in foraging theory. Behavioral Ecology 5:28–34

Yoda K, Kohno H, Naito Y (2004) Development of flight performance in the brown booby. Proceedings of the Royal Society of London Series B: Biological Sciences 271:S240–S242

Zuur AF (2009a) Mixed effects models and extensions in ecology with R, NY: Springer. Springer, New York

Zuur AF (ed) (2009b) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Supplementary

Species biological aspects

Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021). Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997). However, this strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a more important utilization of the '*sit-and-wait*' technique and possibly to vary depending on sites suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the former technique (compared to '*foraging-in-flight*').

Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale migratory movements reaching >4000 km from the colony exploiting continuously warm waters (~18°C). No clear longitudinal seasonality existed in the movements of adults, nonetheless they tended to move westwards in June/July and eastwards in November. The immature birds moved widely in longitude (0° to 135° E), exploiting exclusively warm waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity existed in the movements, except that they also tended to move westwards in June and eastwards in November. Juveniles exhibited very large post-fledging movement capacities over the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal gradient (27° to 47° S). Juveniles birds tended to move westwards first in March-April and temporarily exhibited synchronous individual movements. De Grissac et al. (2016) compared trajectories (i.e. departure direction or orientation toward specific areas) of juveniles and adults and showed that juveniles performed an initial rapid movement taking all individuals away from the vicinity of their native colony, and in a second time performed large-scale movements similar to those of adults during the sabbatical period. High individual variability and no clear differences between juveniles and adults patterns were found, except that adults foraged at significantly higher latitudes. De Grissac et al. (2016) concluded in an overlap in distribution between adults and juveniles due to the extensive area they used and their differences in latitudinal distribution compared to other Procellariiformes species.

Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch 1991). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting important constraints that could compete with breeding (immature birds tend to renew fewer feathers compared to adult breeders), and particularly in females (Weimerskirch 1991). In smaller sized seabirds, a link between moulting pattern and activity parameters was evidenced, resulting in a clear temporal pattern partly explained by moult (Cherel et al. 2016). Recently Gutowsky et al. (2014) suggested that tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could compromise flight from active wing moult during the nonbreeding period and induce changes in daily activity budget during a ‘quasi-flightless’ stage. However, there is no such data for southern albatrosses. Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested it such a compromise. However, adult birds during the non-breeding season appear to spend much more time on the water during winter, suggesting that partial moult may occur at this time, as observed in many other seabird species that have to moult during the non-breeding season and show reduced activity during specific periods that may correspond to moulting (Weimerskirch et al. 2015, 2020).

Table S1 Hypotheses and predictions about the factors driving differences in activity (time spent on water, number and duration of flying bouts, number and duration of water bouts) year-round in Amsterdam albatrosses

	Predictions		
Hypothesis	Time spent on water (%)	Flying bouts (number/duration)	Water bouts (number/duration)
(A) Age and stage specific	Juveniles: increased foraging time/effort and thus lower time spent on water than other stages	Juveniles: increased foraging time/effort and thus longer flying bouts than other stages	Juveniles: increased foraging time/effort and thus shorter water bouts than other stages
(B) Temporal change	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: change in foraging skills (lower time spent on water) corresponding to gradual change with less time sitting on water during the 1st month after fledging Following departure from the colony adjustment in foraging effort or moult constraints	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: change in foraging skills corresponding to gradual change with increasing flying bouts duration and number during the 1st months after fledging Adjustment in foraging effort or moult constraints according to time elapsed since departure	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: change in foraging skills corresponding to gradual change with decreasing water bouts duration and number during the 1st months after fledging Adjustment in foraging effort or moult constraints according to time elapsed since departure
(C) Seasonal environmental change	Progressive adjustment during the months of the year in foraging effort to energetic requirements or moult constraints.	Progressive adjustment during the months of the year in foraging effort to energetic requirements or moult constraints.	Progressive adjustment during the months of the year in foraging effort to energetic requirements or moult constraints.

	Higher time spent on water during moulting	Lower flying bouts duration and number during moulting	Higher water bouts duration and number during moulting
(D) Sex-specific body size	Behavioural difference maintained throughout the cycle: lower time spent on water for females compared to males Alternative prediction: no specific prediction due to trade-off between duration and number of bouts	Behavioural difference maintained throughout the cycle: females sustain shorter flying bouts but more numerous compared to males	Behavioural difference maintained throughout the cycle: females sustain longer water bouts duration but less numerous compared to males

Table S2 Selected models testing for the effects of sex, stage, number of months spent since departure (monthelap: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on) on activity parameters of Amsterdam albatrosses

	Model #	**Study variable**[1]	**Model structure**	**Sample size**
All stages	gamm1	PC1S	~s(monthelap, k = 2) + monthf + stade + sex + s(monthelap, device_code[2], bs = "re")	8094
All stages	gamm2	PC2S	~ s(monthelap, k = 3) + monthf + stade + s(monthelap, device_code, bs = "re")	8094
All stages	gamm3	PC3S	~monthf+stade+sex+s(monthelap,device_code, bs='re')	8094
Juveniles	gamm4	PC1J	~ s(monthelap,k=2)+monthf+s(monthelap,device_code, bs='re')	6161
Juveniles	gamm5	PC2J	~ s(monthelap, k = 2)+monthf+sex+s(monthelap, device_code, bs = "re")	6161
Juveniles	gamm6	PC3J	~monthf+sex+s(monthelap,device_code, bs='re')	6161

[1] First, second and third principal component issued from principal components analyses considering i) all stages combined (PCS) and ii) only juveniles (PCJ); [2] Individuals

Table S3a GAMM results for the first principal components (PC1S; gamm1 see Table S2) of Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.996	149.23	0.000
s(monthelap,device_code)	26.083	14.53	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.48	0.10	4.98	0.000
February	-0.21	0.08	-2.52	0.012
March	-0.60	0.09	-6.94	0.000
April	-0.96	0.09	-10.46	0.000
May	-0.77	0.09	-8.31	0.000
June	-0.77	0.09	-8.16	0.000
July	-0.42	0.09	-4.49	0.000
August	-0.11	0.09	-1.18	0.240
September	0.01	0.09	0.10	0.918
October	0.01	0.09	0.17	0.868
November	-0.01	0.09	-0.09	0.929
December	-0.08	0.09	-0.90	0.367
Immatures	-0.50	0.09	-5.76	0.000
Juveniles	-0.63	0.07	-9.69	0.000
Males	0.33	0.05	6.22	0.000

Table S3b GAMM results for the second principal components (PC2S; gamm2 see Table S2) of Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.001	0.504	0.478
s(monthelap,device_code)	27.107	39.991	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.15	0.10	-1.53	0.126
February	0.13	0.08	1.71	0.088
March	0.16	0.08	2.00	0.046
April	0.42	0.08	5.03	0.000
May	0.40	0.08	4.99	0.000
June	0.25	0.08	3.16	0.002
July	0.23	0.08	2.92	0.004
August	0.26	0.08	3.40	0.001
September	0.48	0.08	6.22	0.000
October	0.35	0.08	4.57	0.000
November	0.34	0.08	4.41	0.000
December	0.19	0.08	2.49	0.013
Immatures	-0.12	0.08	-1.57	0.116
Juveniles	-0.18	0.06	-2.96	0.003

Table S3c GAMM results for the third principal components (PC3S; gamm3 see Table S2) of Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap,device_code)	26.52	16.58	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.34	0.06	5.37	0.000
February	-0.22	0.06	-3.43	0.000
March	-0.07	0.06	-1.08	0.279
April	-0.10	0.07	-1.53	0.127
May	0.00	0.06	0.05	0.958
June	0.05	0.06	0.87	0.385
July	0.02	0.06	0.39	0.694
August	-0.04	0.06	-0.70	0.483
September	-0.06	0.06	-0.93	0.355
October	-0.10	0.06	-1.58	0.012
November	-0.16	0.06	-2.57	0.010
December	-0.23	0.06	-3.70	0.000
Immatures	-0.27	0.06	-4.61	0.000
Juveniles	-0.45	0.05	-9.12	0.000
Males	-0.14	0.04	-3,39	0.000

Table S4a GAMM results for the first principal components (PC1J; gamm4 see Table S2) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap) and month of the year. Reference value is January.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.922	24.12	0.000
s(monthelap,device_code)	6.506	12.20	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.10	0.09	-1.16	0.247
February	0.20	0.09	2.30	0.021
March	-0.13	0.09	-1.51	0.132
April	-0.27	0.09	-3.12	0.002
May	-0.16	0.09	-1.91	0.056
June	0.06	0.09	0.71	0.475
July	0.59	0.09	6.66	0.000
August	0.68	0.09	7.66	0.000
September	0.47	0.09	5.26	0.000
October	0.22	0.09	2.47	0.013
November	-0.05	0.09	-0.50	0.616
December	-0.04	0.09	-0.45	0.653

Table S4b GAMM results for the second principal components (PC2J; gamm5 see Table S2) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap) and month of the year. Reference value is January.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.000	2.40	0.122
s(monthelap,device_code)	6.813	55.91	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.05	0.12	-0.43	0.668
February	-0.27	0.08	-3.54	0.000
March	-0.14	0.08	-1.88	0.061
April	0.12	0.07	1.61	0.107
May	0.08	0.08	1.02	0.306
June	0.01	0.08	0.14	0.886
July	0.08	0.08	1.05	0.293
August	0.12	0.08	1.47	0.141
September	0.30	0.08	3.84	0.000
October	0.18	0.08	2.33	0.020
November	0.19	0.08	2.44	0.015
December	0.20	0.08	2.49	0.013
Male	-0.17	0.06	-2.78	0.005

Table S4c GAMM results for the third principal components (PC3J; gamm5 see Table S2) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year and sex. Reference value are January and females.

Variable	Smoother edf	F-test	p-value
s(monthelap,device_code)	7.724	19.37	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.04	0.05	-0.77	0.444
February	-0.10	0.06	-1.59	0.113
March	-0.13	0.06	-2.19	0.029
April	-0.06	0.06	-0.94	0.349
May	0.02	0.06	0.37	0.715
June	0.13	0.06	2.11	0.035
July	0.02	0.06	0.25	0.802
August	0.00	0.06	0.01	0.992
September	0.00	0.06	0.01	0.996
October	-0.04	0.06	-0.59	0.556
November	-0.06	0.07	-0.85	0.395
December	0.02	0.06	0.34	0.735
Male	0.10	0.05	1.89	0.059

FIGURES

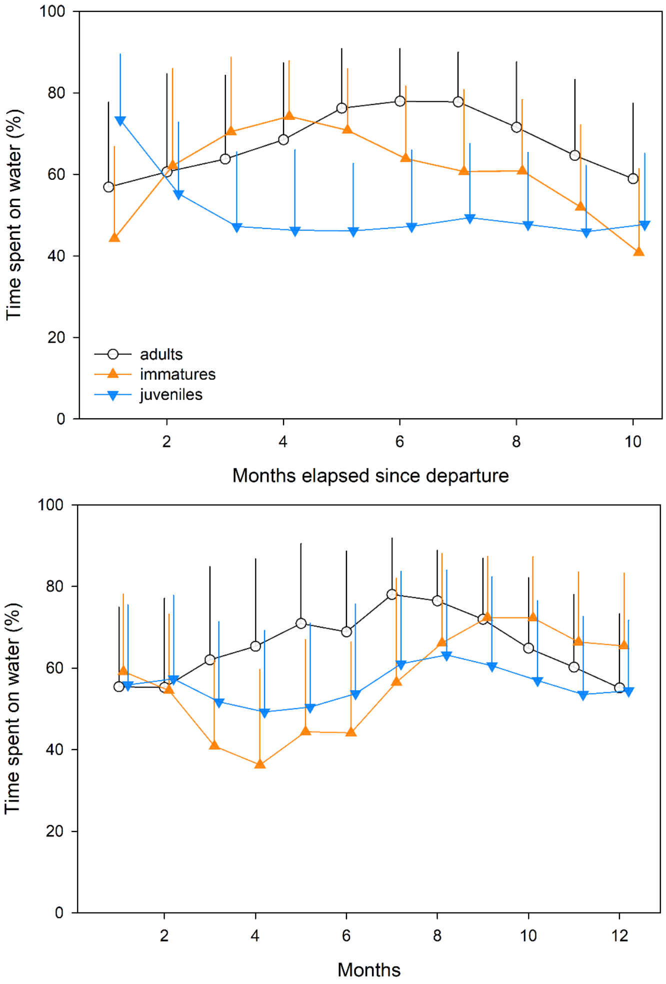


Figure S1 Daily proportions of time spent on water depending on stage (juveniles, immatures and adults) for every month since departure from the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

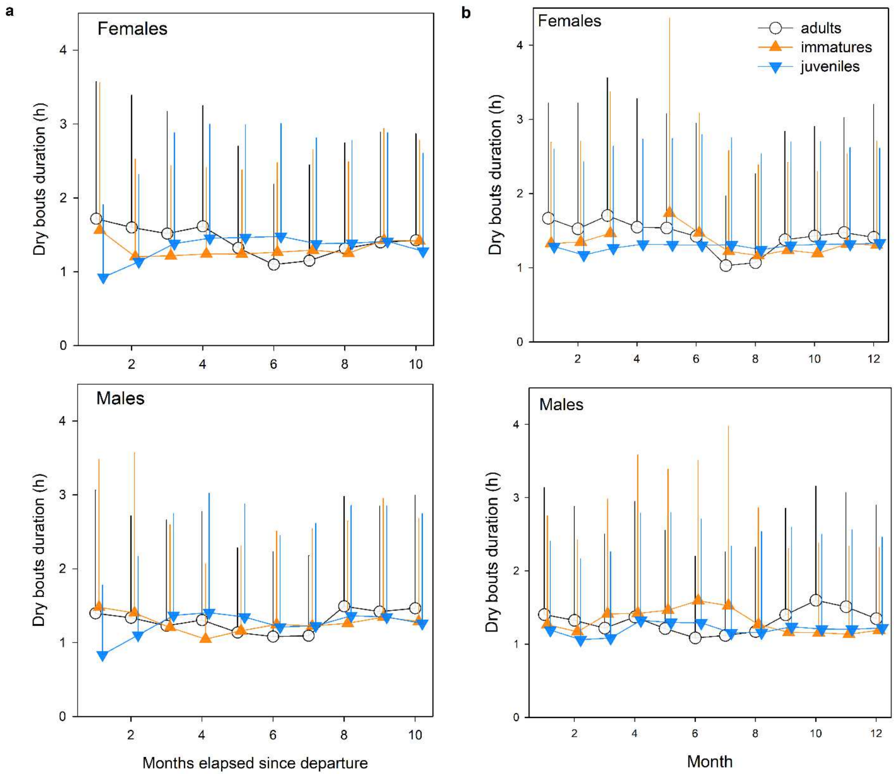


Figure S2 Daily flying bouts duration (dry bouts in hours) depending and on sex (females and males) and on stage (juveniles, immatures and adults) for a) time elapsed since departure from the colony expressed in month (left panel) and for b) each month of the year (right panel). One side error bars represent ± 1 sd

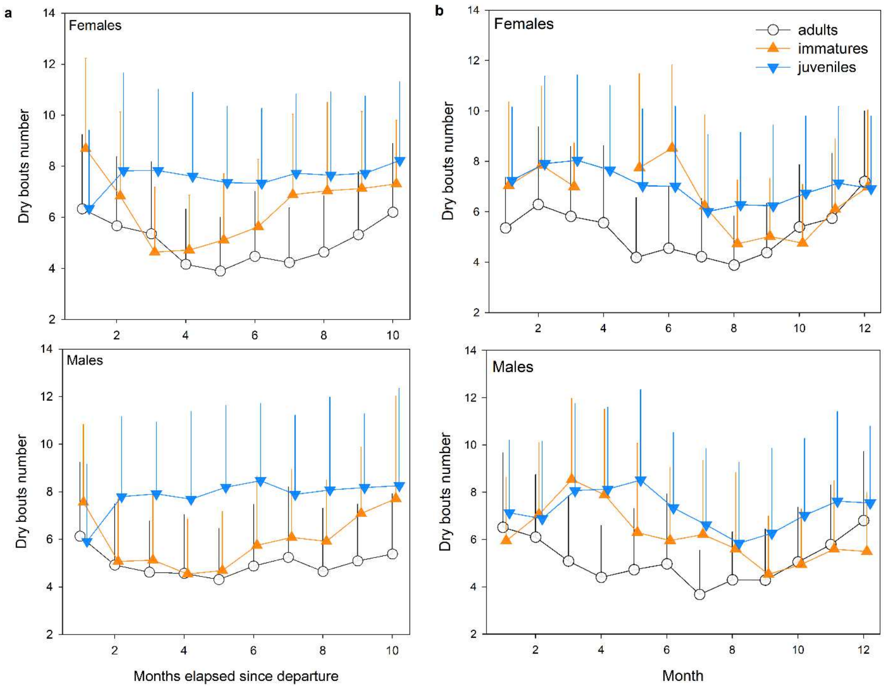
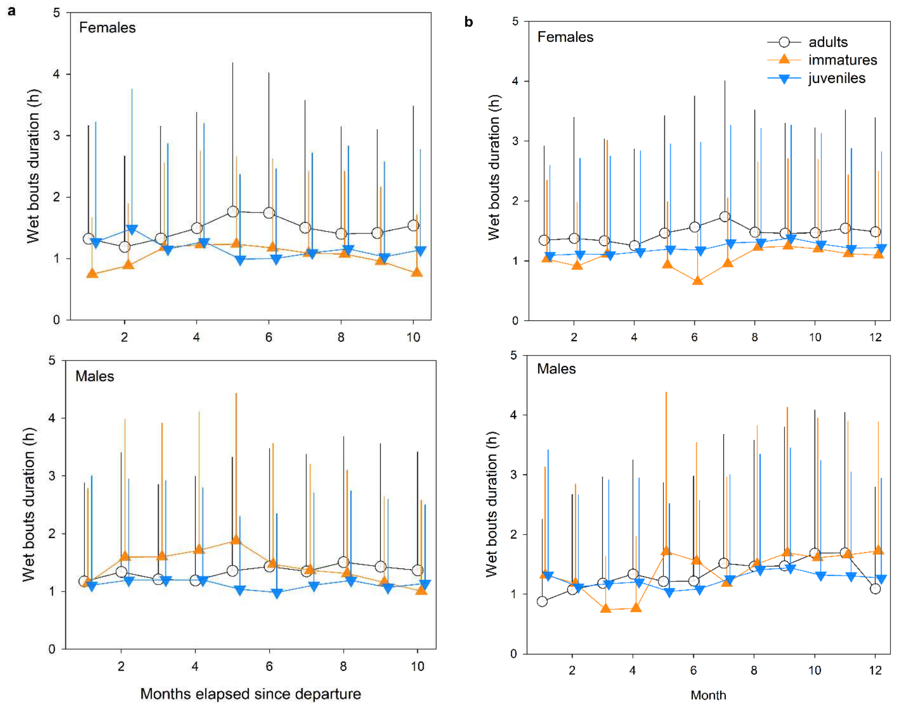


Figure S3 Daily flying bouts number (dry bouts) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd



1529

1530 Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures
1531 and adults) and on sex (females and males) for every month since departure of the colony (upper panel)
1532 and for each month of the year (lower panel). Error bars represent ± 1 sd

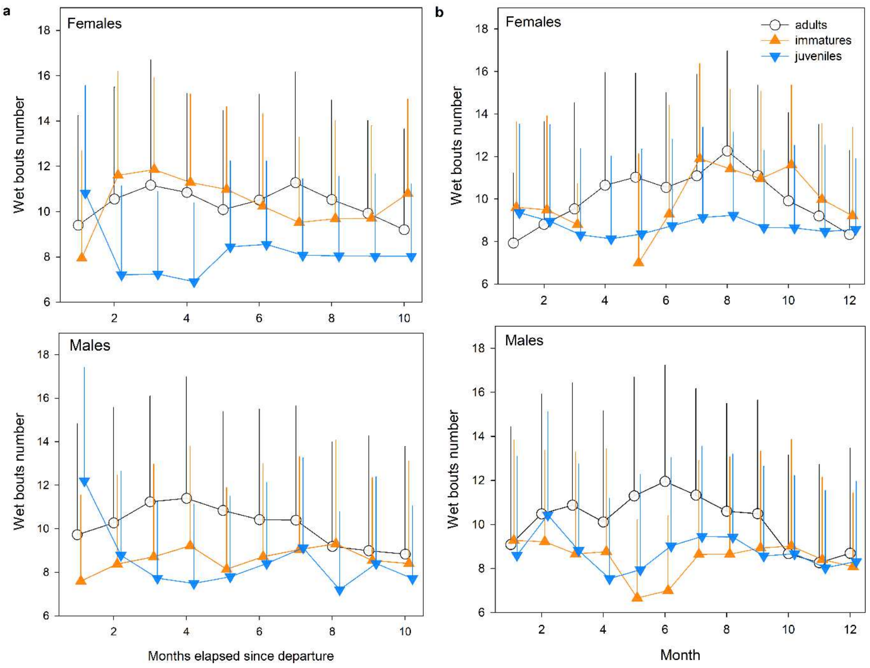


Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

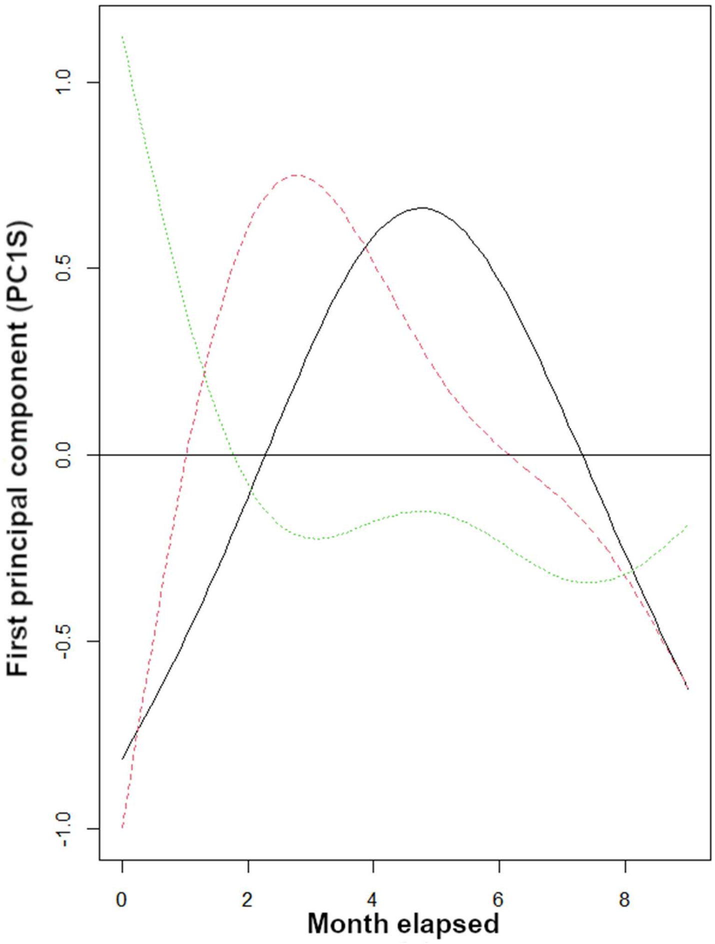


Figure S6 Modeled first axis of principal components analysis of activity parameters of all stages (i.e. adult (plain black line), immature (dashed red line) and juvenile (dotted green line)) of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model

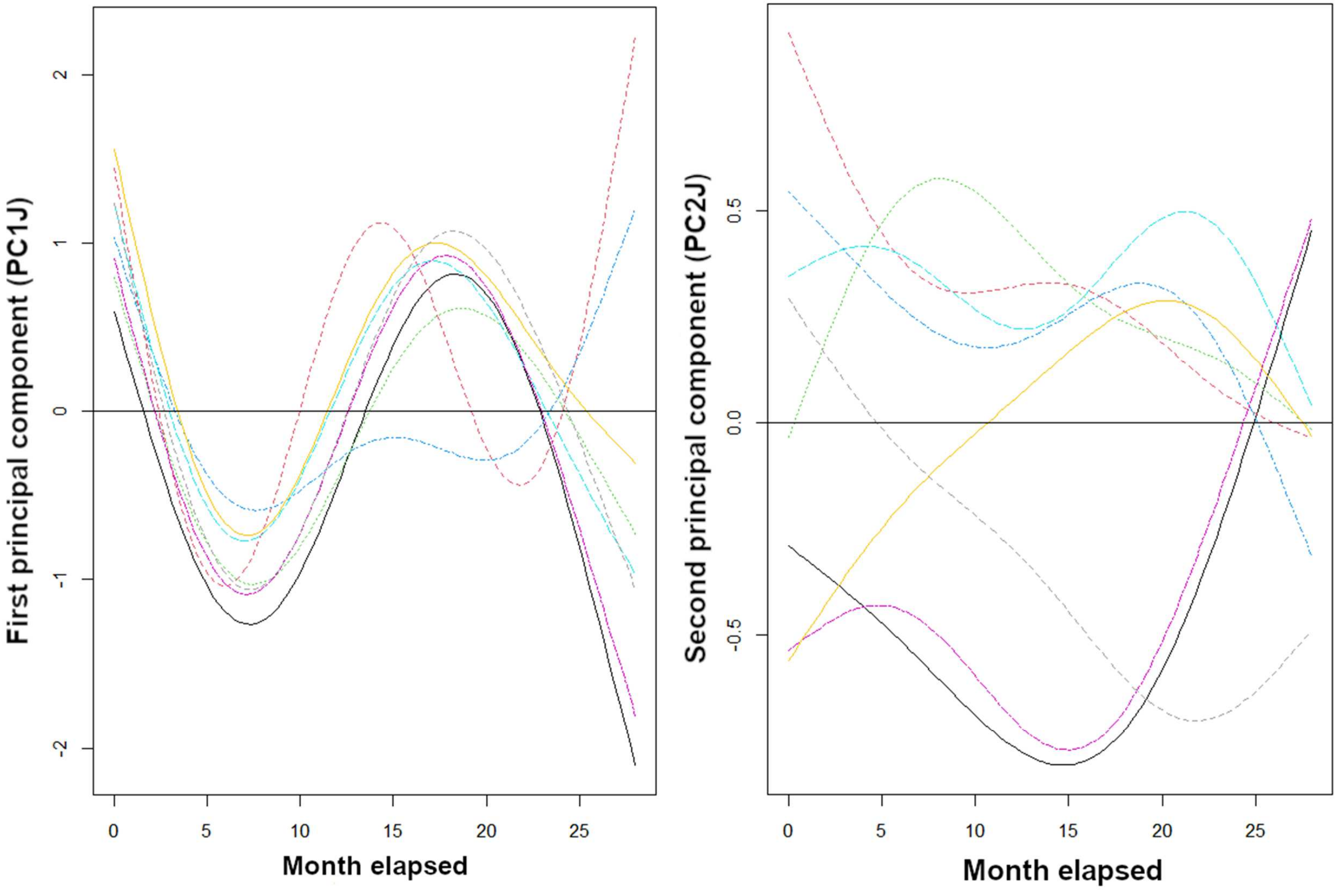


Figure S7 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs obtained using random intercepts and slopes (each coloured line representing an individual). Line corresponds to estimated smoother from the GAMM models

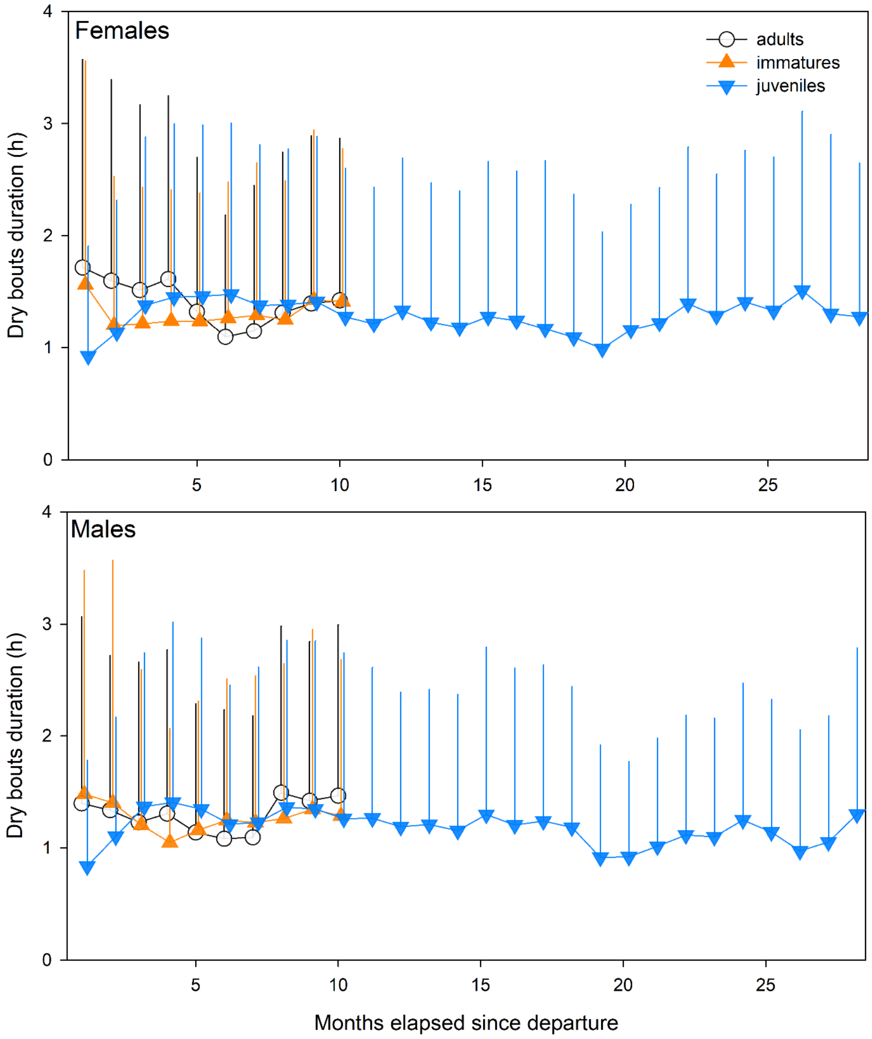


Figure S8 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

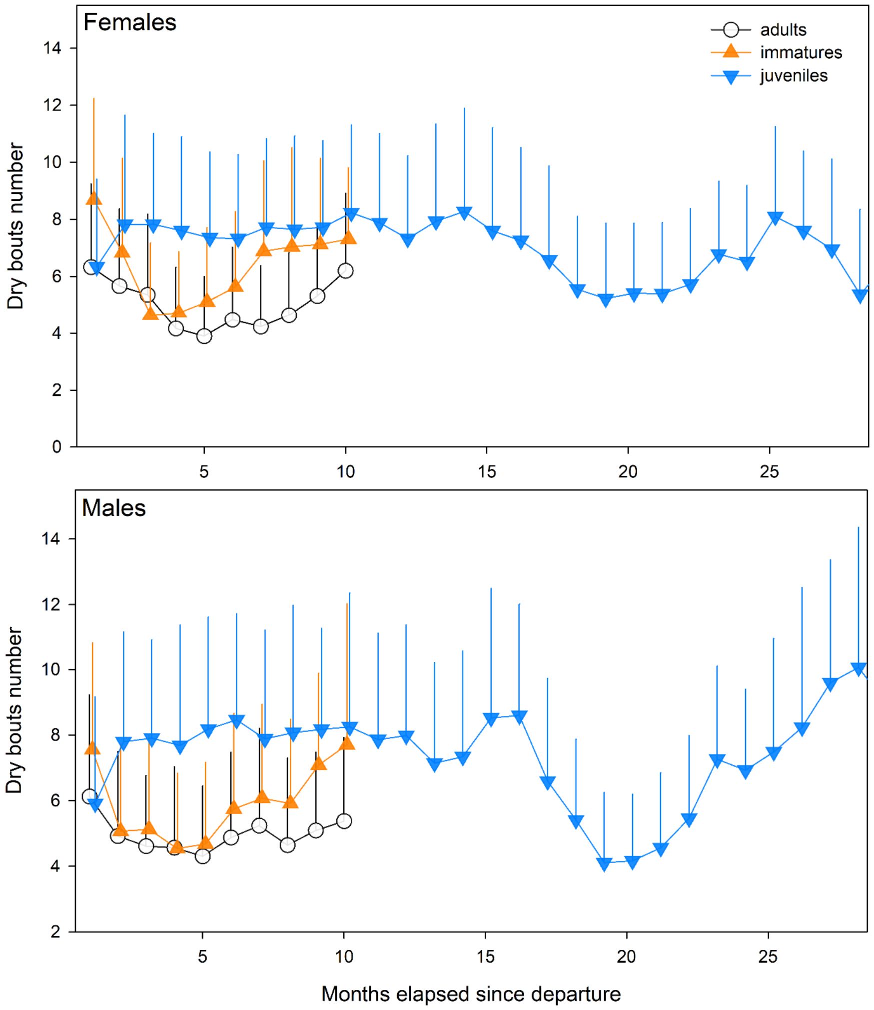


Figure S9 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

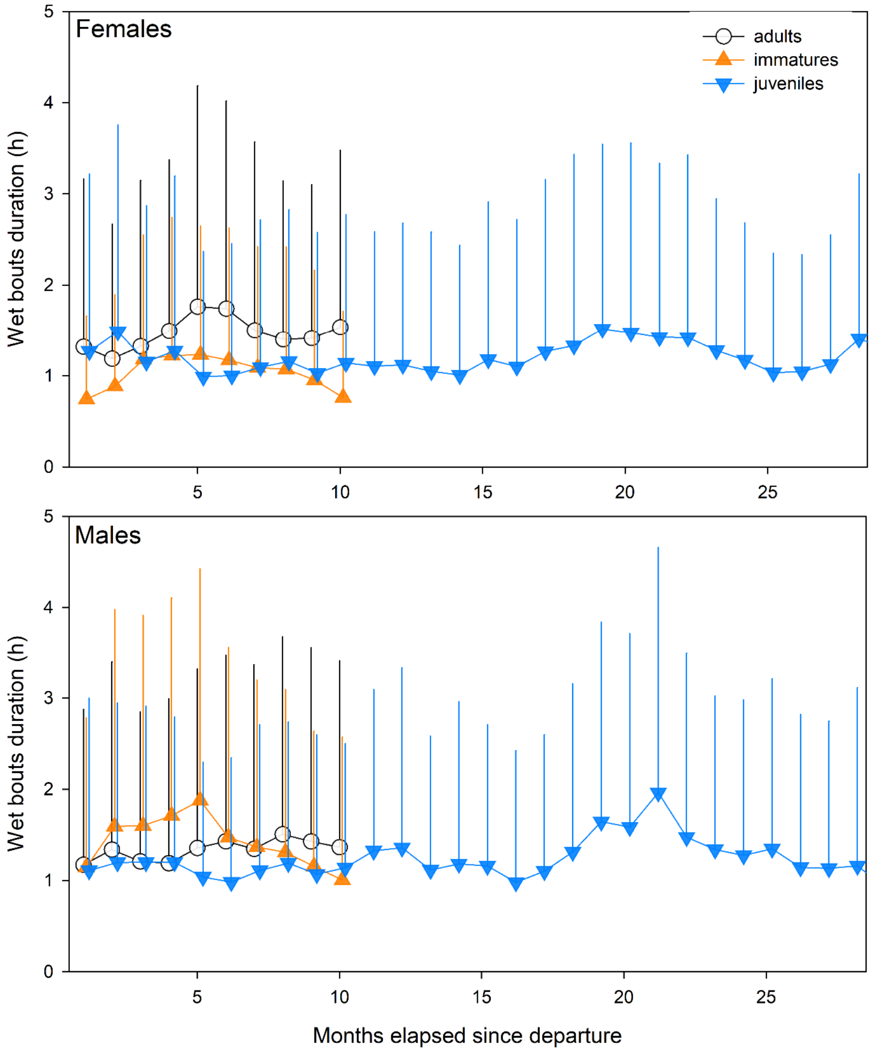


Figure S10 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

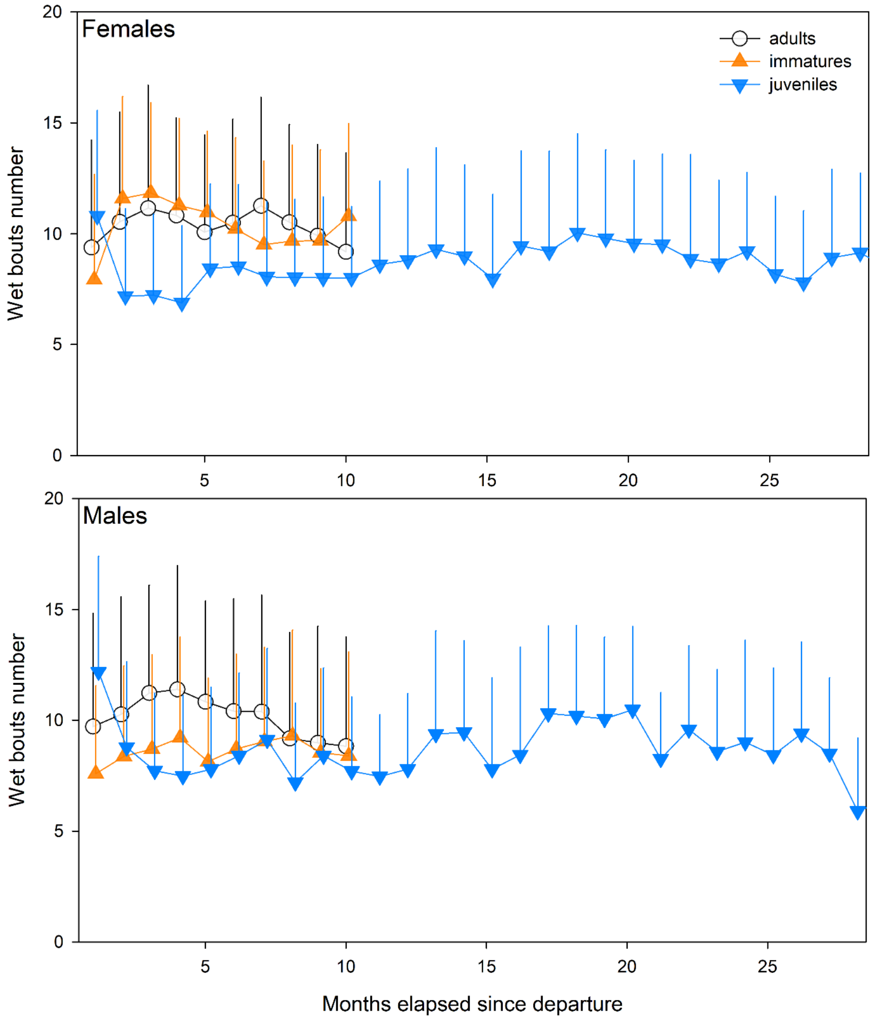
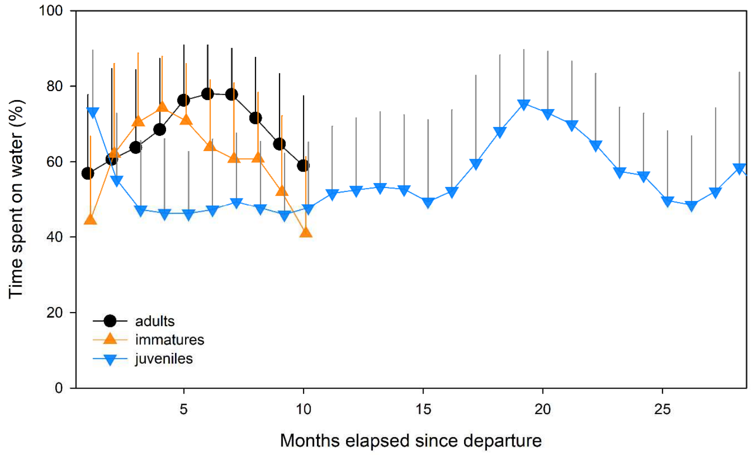


Figure S11 Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

a



b

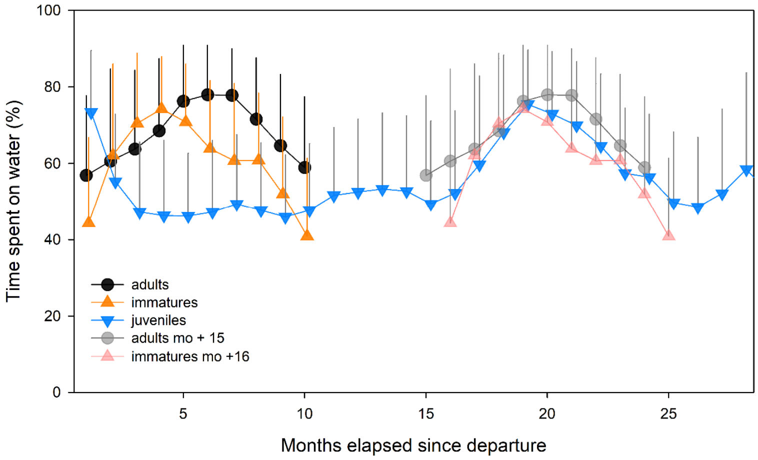


Figure S12 Daily proportions of time spent on water for every month since departure of the colony for juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel) and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error bars represent ± 1 sd

REFERENCES

Cherel Y, Quillfeldt P, Delord K, Weimerskirch H (2016) Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. Front Ecol Environ 4:1–16

de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. Sci Rep 6:26103

Delord K, Barbraud C, Bost CA, et al (2013) Atlas of top predators from the French Southern Territories in the Southern Indian Ocean. http://www.cebc.cnrs.fr/ecomm/Fr_ecomm/ecomm_ecor_OI1.html

Ellis HI, Gabrielsen GW (2002) Energetics of free-ranging seabirds. In: Seabirds energetics, Whittow, G. C. and Rahn, H. Plenum Press, N.Y., pp 359–408

Furness RW (1988) Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed albatross Diomedea chlororhynchos. J Zool 215:719–727

Gutowsky SE, Gutowsky LF, Jonsen ID, et al (2014) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. Mov Ecol 2:23–23

Langston NE, Rohwer S (1996) Molt-breeding tradeoffs in albatrosses : life history implications for big birds. Oikos 76:498–510

Louzao M, Wiegand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Mov Ecol 2:1–15

Murphy ME (1996) Energetics and nutrition of molt. In: Avian energetics and nutritional ecology. Springer, pp 158–198

Nevitt GA, Losekoot M, Weimerskirch H (2008) Evidence for olfactory search in wandering albatross, Diomedea exulans. Proc Natl Acad Sci 105:4576–4581

Pajot A, Corbeau A, Jambon A, Weimerskirch H (2021) Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. J Avian Biol 52:

Peery MZ, Henkel LA, Newman SH, et al (2008) Effects of rapid flight-feather molt on postbreeding dispersal in a pursuit-diving seabird. The Auk 125:113–123

Phalan B, Phillips RA, Silk JR, et al (2007) Foraging behaviour of four albatross species by night and day. Mar Ecol Prog Ser 340:271–286

Thiebot J-B, Delord K, Marteau C, Weimerskirch H (2014) Stage-dependent distribution of the critically endangered Amsterdam albatross in relation to Economic Exclusive Zones. Endanger Species Res 23:263–276

Weimerskirch H (1991) Sex-specific differences in molt strategy in relation to breeding in the wandering albatross. Condor 93:731–737

Weimerskirch H, de Grissac S, Ravache A, et al (2020) At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. Mar Ecol Prog Ser 633:225–238

Weimerskirch H, Tarroux A, Chastel O, et al (2015) Population-specific wintering distributions of adult south polar skuas over the three oceans. Mar Ecol Prog Ser 538:229–237

Weimerskirch H, Wilson RP, Lys P (1997) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Mar Ecol Prog Ser 151:245–254

TITLE

The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird

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Abstract

The transition to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher mortality including that of inadequate/inferior foraging skills compared to adults, young naï~~ï~~ve individuals combining lack of experience and physical immaturity. Thus a change in behaviour, resulting in an improvement of skills acquired from growing experience, is expected to occur during a period of learning through the immaturity phase. Very few studies have investigated the ontogeny of foraging behaviour over long periods of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over several years. We investigated the foraging behaviour, through activity patterns, during the ~~successive~~ three life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naï~~ï~~ve juveniles, immatures and adults. Naïve j~~J~~uveniles ~~naïve birds~~ during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, ~~higher duration~~longer and more numerous bouts on water, ~~and lower duration~~shorter and ~~less numerous~~fewer flying bouts). Patterns of activity parameters in juveniles after independence suggested a progressive change of foraging performances during the first two months since fledging. ~~Juveniles reached similar activity values to those of immatures and adults as early as the 2nd -3rd months since independence, suggesting a progressive improvement of foraging performances during the first two months since fledging.~~ We found sex differences ~~support for the body-size hypothesis with respect to sex differences~~ in activity parameters according to time ~~elapsed~~ since departure from the colony and month of the year, consistent with the important sexual dimorphism in the Amsterdam albatross. ~~Whatever th~~Regardless ~~e~~of life stage considered, activity parameters exhibited temporal variability reflecting the modulation of foraging behaviour. This variability is discussed ~~possibly~~ in light of~~linked to~~ both extrinsic (i.e. environmental conditions such as variability in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew during moult) factors).

Keywords: activity data loggers; foraging behaviour; southern Indian Ocean; Amsterdam albatross; *Diomedea amsterdamensis*

Introduction

The transition from parental food dependency to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals (Mushinsky et al. 1982; Margrath and Lill 1985; Martin and Bateson 1985; Marchetti and Price 1989; Langen 1996; Burns et al. 2004) and is increasingly documented in a wide range of taxa (reptiles, birds, and some mammals).~~ Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals (Ydenberg 1989; Menu et al. 2005; Oppel et al. 2015; Cheng et al. 2019). Several hypotheses have been proposed to explain higher mortality observed for young individuals compared to adults (Healy et al. 2019). One of the most~~ A widely accepted hypotheses is inadequate/inferior foraging skills of juveniles compared to adults, young naï~~i~~ve individuals combining lack of experience and physical immaturity (Lack 1954; Daunt et al. 2007). Thus, a change in behaviour, resulting ~~in~~ from an improvement of skills acquired from increasing experience is expected to occur during a period of learning through the immaturity phase. Learning often refers to stimulus-response associative learning ('trial and error'; Ruaux et al. 2020), although other forms of learning (such as social learning or imprinting) are also taken into account when considering the ontogeny of complex behaviours (Heyes 1994; Wynn et al. 2020). Such a learning process has been studied on various taxa from insects to primates (Bruner 1972; Caubet et al. 1992; Dukas 2006; Rapaport and Brown 2008). ~~Learning often refers to stimulus-response associative learning ('trial and error'; (Ruaux et al. 2020)), although other forms of learning (such as social learning or imprinting) are also taken into account when considering the ontogeny of complex behaviour (Heyes 1994; Wynn et al. 2020).~~

Juvenile birds are known to undertake vagrant erratic journeys during the post-fledging period ~~especially~~ in passerines (Naef-Daenzer and Grüebler 2008; Becker 2014; Evans 2018; Boynton et al. 2020), in raptors (Urios et al. 2010; Krüger et al. 2014; Harel et al. 2016) and in seabirds (Riotte-Lambert and Weimerskirch 2013; Collet et al. 2020). Recent studies highlighted that the flight capacities and foraging behaviour of

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juveniles differed from those of adults in storks (Rotics et al. 2016), raptors (Harel et al. 2016; Nourani et al. 2020) or seabirds (Ydenberg 1989; Péron and Grémillet 2013; de Grissac et al. 2017; Corbeau et al. 2020). Most flight components were found to improve over time to tend towards those of adults (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2017; Corbeau et al. 2020).

However, studies focusing on the foraging behaviour of juveniles remain scarce because of the difficulty to obtain individual tracking data for long periods, especially for long-lived pelagic seabirds with deferred maturity. Moreover, existing studies comparing flight capacities and foraging behaviour between juveniles and adults in such species only collected data during the first few months that juveniles spent at sea. Since juveniles may spend several years at sea before returning to a colony to breed, our understanding of the ontogeny of flight capacities and foraging behaviour remains fragmentary.

The Amsterdam albatross *Diomedea amsterdamensis* is a large and long-lived pelagic seabird with an extended immaturity stage (~ 9 years Rivalan et al. (2010)). Similarly to a closely related species, the wandering albatross *D. exulans*, their foraging strategy relies on very low flight costs as a result of their dynamic soaring flight, whereby individuals optimize the orientation of their movement with wind direction to maximize the daily distance covered (Pennycuick 1982). During initial post-fledging dispersal juveniles ~~disperse~~ wander alone over very long distances from their colony. At sea distribution during every stage of the life-cycle of Amsterdam albatross was studied by Thiebot et al. (2014) and de Grissac et al. (2016) who compared flight trajectories (i.e. departure direction or orientation toward specific areas)~~movement patterns~~ of juveniles and adults~~, namely trajectories (i.e. departure direction or orientation toward specific areas)~~. Both studies concluded on slight differences among stages in distribution due to the extensive area they used. However, foraging behaviour is known to be constrained by intrinsic factors such as sex, age, reproductive status and body size across a wide range of taxa and hence play a key role in shaping activity (King 1974; Alerstam and Lindström 1990; Wearmouth and Sims 2008). To understand the ~~potentially~~ changes in foraging proficiency according to experience (life-history stages), longitudinal studies of individuals spanning critical periods of their lives are thus required. Advances in animal-borne instrumentation enable key component of foraging behaviour such as foraging effort and activity to be recorded over long periods.

In this study, we benefited from a unique dataset of different life stages (juveniles, immatures and adults) and a remarkable duration (up to 28 months for juveniles) to characterise and compare the behaviour changes when birds leave the colony for several months (immatures and adults) or years (juveniles). ~~In this study~~Here, ~~w~~We ~~compare~~ analyse the foraging behaviour, through activity patterns, of naï~~i~~ve juveniles (first years of independence at sea), immatures (individuals that never bred, age 2-10 years) and adults (individuals that bred at least once, age 8-28 years) of Amsterdam albatross (Table 1). By using miniaturized activity loggers (Global Location Sensing; GLS) to infer foraging behaviour (activity) throughout the successive life stages we addressed the following questions: i) do individuals belonging to different life-stages behaved differently? ii) are there differences in activity patterns between life-stages~~, namely time spent on water and flying bouts~~, and are there detectable progressive changes? However, the loggers used does not yet allow to have longitudinal data and to cover the entire period until an individual is recruited into the population as a breeding adult, i.e. at least 8 years.

Previous knowledge of the ecology of large albatrosses and Amsterdam albatross described above provides a practical framework for testing predictions about variability in foraging behaviour associated with ~~sex,~~ stage, time elapsed since departure from the colony, ~~and~~ seasons and sex which are summarised in Table S1. Given the overlap of spatial distribution between life-stages (not presented here but see Thiebot et al. 2014; de Grissac et al. 2016; Pajot et al. 2021) we predicted that juveniles would compensate for any lack of foraging proficiency by increasing foraging effort and time (i.e. lower time spent on water and longer flying bouts, in other words decreasing time sitting on water and longer and more numerous bouts in flight; Hypothesis (~~B~~A), Table S1~~2~~). We also predicted ~~sharp~~ changes in activity following fledging of juveniles from the colony followed by more progressive changes. Based on results found on fledglings wandering albatross (Riotte-Lambert and Weimerskirch 2013; Pajot et al. 2021) showing that juveniles reached some adult foraging capacities in less than two months, we predicted that ~~important~~ changes should be detected in activity parameters early after the juvenile left the colony (within few first months). Overall, juveniles should show ~~higher~~ contrasted foraging effort (i.e. longer time spent on water, shorter flying effort with fewer and shorter flying bouts) just after fledging compared to other life-stages ~~(i.e. lower time spent on water, longer flying bouts and shorter water bouts)~~. Due to seasonal changes in food availability individuals will face at sea after leaving the colony and the alleviation of energetic constraints linked to reproduction (for breeding adults) or to alternate foraging trips at sea and period on land for pair bonding and mating display (for immature birds), we predicted that adjustments of activity will occur according to the time spent (i.e. in months elapsed) since the departure of individuals from the colony (Hypothesis (~~C~~B), Table ~~2~~S1). In juveniles, we predicted early and rapid changes after fledging and then more progressive changes. Due to environmental changes occurring throughout the seasons we predicted temporal (i.e. related to the month of the year) changes in activity parameters for all life-stages (Hypothesis (~~D~~C), Table ~~2~~S1). Although food availability may be lower during winter, foraging effort may also be reduced when adults and immatures are moulting (Weimerskirch 1991). Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch 1991). Partial moulting is suspected to occur outside the breeding period and to result in reduced activity (i.e. more time spent on the water; Weimerskirch et al. 2015, 2020). We therefore predicted a period of reduced activity that differs according to the life-stages and may be confounded by seasonal variability (Hypothesis (C). Lastly, due to sex differences in flight performances (Shaffer et al. 2001; Clay et al. 2020), specifically, due to their higher wing loading, males should both maintain longer flying effort, and be more likely to minimize the number of flying bouts than females. Thereupon, and based on results on wandering albatross (Riotte-Lambert and Weimerskirch 2013), similar pattern should be maintained outside the breeding period. We thus predicted differences in foraging behaviour between sexes (i.e. time spent on water, duration and number of flying and water bouts; Hypothesis (~~A~~D), Table ~~2~~S1).

Materials and methods

Study species and data loggers

Amsterdam Island (37° 50’ S; 77° 33’ E) is located in the subtropical part of the southern Indian Ocean. In this oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder sub-Antarctic waters (Belkin & Gordon 1996). Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021; see Supplementary). Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred as ‘*foraging-in-flight*’ is the lowest energy consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997b). However, this strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014), leading to a more important utilization of the ‘*sit-and-wait*’ technique and possibly to vary depending on sites suggesting ~~considerable~~ behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the former technique (compared to ‘*foraging-in-flight*’).

The Amsterdam albatross, like other great albatrosses, is a biennial breeder (Roux et al. 1983; Jouventin et al. 1989), with high survival during juvenile, immature and adult phase (Rivalan et al. 2010). The adults that raised a chick successfully do not start a new breeding cycle after chick fledging, but remain at sea for a sabbatical period (~1 yr; Table 1; Rivalan et al. 2010). However, early failed breeders may start to breed the following year (Rivalan et al. 2010). Immature birds may visit the colony when they are 4−7 yrs old, but generally only start breeding at 9 yrs old (Table 1; Weimerskirch et al. 1997a). Juvenile birds fledge and migrate independently from the adults in January (Table 1). Exact fledging dates were not known for juveniles but were assessed from activity pattern as juvenile birds land on water quickly after leaving the colony (Weimerskirch et al. 2006). Amsterdam albatrosses were monitored annually since 1983 and all individuals were individually marked (numbered stainless steel and plastic engraved colour bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age (79 individuals since the beginning of the study) and chicks of the year were banded, weighed (body mass ± 50 g using a Pesola® spring balance) and measured (wing length ± 1 mm with a ruler, tarsus length, bill length, and bill depth ± 0.1 mm with calipers).

Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale ~~dispersal~~ migratory movements (*sensu* Weimerskirch et al. 2015a) reaching >4000 km from the colony exploiting continuously warm waters (~18°C). No clear longitudinal seasonality existed in the movements of adults, nonetheless they tended to move westwards in June/July and eastwards in November. The immature birds moved widely in longitude (0° to 135° E), exploiting exclusively warm waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity existed in the movements, except that they also tended to move westwards in June and eastwards in November. Juveniles exhibited very large ~~dispersal~~ migratory capacities over the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal gradient (27° to 47° S). Juveniles birds tended to ~~disperse~~ migrate westwards first in March-April and temporarily exhibited synchronous individual movements. De Grissac et al. (2016) compared trajectories (i.e. departure direction or orientation toward specific areas) of juveniles and adults and showed that juveniles performed an initial rapid movement taking all individuals away from the vicinity of their native colony, and in a second time performed large-scale movements similar to those of adults during the sabbatical period. High individual variability and no clear differences between juveniles and adults patterns were found, except that adults foraged at significantly higher latitudes. De Grissac et al. (2016) concluded in an overlap in distribution between adults and juveniles due to the extensive area they used and their differences in latitudinal distribution compared to other Procellariiformes species.

~~Global Location Sensing (~~GLS~~)~~ are archival light-recording loggers ~~were~~ used to study activity of birds over periods lasting up to ~ 2 years. GLSs record the ambient light level every 10 min, from which local sunrise and sunset hours can be inferred to estimate location every 12 h (Wilson et al. 1992). GLS also recorded saltwater immersion data ~~Immersion loggers~~by ~~tested~~ testing for saltwater immersion every 30 s, storing the number of samples wet (>0) at the end of each 10 min period. We used saltwater immersion to estimate daily activity budget. Despite the higher mean spatial error of location estimates with these devices (over 100 km; Phillips et al. (2004a)), GLS loggers allowed us to track the birds for prolonged periods with minimal disturbance to them. We considered the following stages regarding the year of GLS deployment (see Table 1): juvenile, as a fledgling equipped with a GLS just before leaving the colony for the first time; immature, as a non-breeding young bird that had never bred equipped with a GLS when visiting the colony; adult, as a breeding adult equipped with a GLS during the incubation or brooding period which successfully fledged a chick and thereafter took a sabbatical year. To date, we have retrieved 40 of the 50 GLS loggers deployed in total over 4 years, from which 33 individual tracks were estimated (Table 2). Our original aim was to collect activity data over the three life-stages on a long period of time

(>1 year). These data are available from a total of 10 adults tracked throughout their sabbatical period, 13 immature birds and 10 juvenile birds (up to 3.2 years).

Data processing

The raw immersion data were obtained from testing saltwater immersion every 30 s, the GLS storing the number of samples wet (> 0) at the end of each 10 min period. The data were values from 0 (no immersion or dry, in flight or sitting on the ground) to 200 (permanently immersed in sea water or wet), indicating the number of 3 s periods during 10 min blocks when the sensor was immersed in saltwater. Loggers recorded proportion of time in seawater at 10 min intervals, which we summarized as hours in the water per day (hereafter time spent on water~~PROWATER~~; 10 min blocks immersion data > 0). This measure is a reliable proxy of foraging effort linked to foraging behaviour of the species which enters the water principally to forage (Weimerskirch and Guionnet 2002). Additionally, the duration of the bouts spent entirely immersed (10 min blocks immersion data = 200) was calculated daily (hereafter referred as wet bouts duration~~WETBOUTS~~). Conversely, when birds are not on land, the time spent dry was interpreted as flying (and thus not feeding). The duration of the bouts spent entirely dry (10 min blocks immersion data = 0) was calculated daily (hereafter referred as dry bouts duration~~DRYBOUTS~~). Additionally the numbers of bouts (number of wet bouts -sitting on water-~~on water: WETBOUTSNB~~ and of dry bouts -flying~~: DRYBOUTSNB~~) were obtained daily. Although the loggers integrated activity within each 10 min block and so did not provide the exact timing of landings and take-offs, Phalan et al. (2007) found for comparative purposes that bouts defined as a continuous sequence of 0 values for flight (dry) and a sequence of values of 1 or greater for wet bouts, were suitable proxies for activity.

To select the data corresponding to periods spent at sea after leaving the breeding site, we used the following criteria on activity to define the departure time from the colony for each stage: 1) juveniles, the first bout spent on seawater (wet bouts duration~~WETBOUTS~~) > 1h based on PTT tracking data

(Weimerskirch et al. unpublished data); 2) immatures and adults, the last bout spent flying (dry bouts duration~~DRYBOUTS~~) > 12h based on PTT tracking data (Weimerskirch et al. unpublished data). Using these criteria we obtained departure months as follows: 1) the juveniles fledged from the colony from January to March, 2) the immatures left between April and August, and 3) the departures of sabbatical adults were spread over two periods, first between December and February and then from May to July.

Statistical analyses

~~Differences between sexes in body measurements were tested using Student's t-tests and Wilcoxon rank tests (see Supplementary A).~~

Variation in activity parameters

The aim was to determine~~evaluate~~ whether distinct foraging behaviours could~~an~~ be detected across the patterns of variation~~various aspects~~ of wet/dry data~~dynamics~~, and then to appraise how ~~use of~~ these behaviours varied~~y~~ over time and among individuals. First, t~~T~~o deal with the fact that wet/dry metrics~~some explanatory variables~~ were interrelated~~might covary~~ (number of wet bouts sitting on water and time spent on water, wet bouts duration and dry bouts duration, wet bouts number and dry bouts number) and to avoid ~~unnecessary~~ redundancy, we ran principal components analyses (PCA built with the 'PCA' function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe behaviours using gradients of activity we ran PCA for i) all stages (PCS; based on activity data collected during the first ten months post-departure) and for ii) juveniles only, as an additional goal was to determine changes in activity patterns during the first two years of life (PCJ; based on activity data collected during the first twenty-nine months post-departure).

Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance. The first principal component (PC1S) explained 41.5% of the total variance, and correlated positively with time spent on water (r = 0.97) and negatively with dry bouts number (r = -0.79). The second principal component (PC2S) explained 32.5% of the variation and correlated positively with wet bouts duration (r = 0.79) and negatively with wet bouts number (r = -0.75). The third principal component (PC3S) explained 20.2% of the variation and correlated positively with dry bouts duration (r = 0.74) and negatively with dry bouts number (r = -0.44).

Considering juveniles, the first three principal component (PCJ) explained 92.2% of the total variance. The first principal component (PC1J) explained 42.3% of the total variance, and correlated positively with time spent on water (r = 0.98) and negatively with dry bouts number (r = -0.76). The second principal component (PC2J) explained 32.2% of the variation and correlated positively with wet bouts duration (r = 0.72) and negatively with wet bouts number (r = -0.75). The third principal component (PC3J) explained 20.7% of the variation and correlated positively with dry bouts duration (r = 0.48) and negatively with dry bouts number (r = -0.46) and wet bouts duration (r = -0.46).

Second, w~~W~~e ~~then ~~used generalized additive mixed~~ additive~~ models (GAMMs, built with the ‘gam’ function, itsadug and mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with each of the three first axe~~i~~s of the PCA~~principal components analyses~~ as the dependent variable. We separately ran models testing for variability in activity parameters i) for all stages combined (PCS) and ii) for juveniles (PCJ), based on different duration of datasets (28 months since departure for juveniles and 9 months since departure for immatures and adults; see Supplementary; Table S2). Thus, for ~~all stages combined~~ i) we considered the lowest number of months elapsed since departure available (9 months since departure). ~~To investigate the causes of variability of the activity parameters during 24h (sitting on water – time spent on waterPROPWATER, wet bouts durationWETBOUTS and dry bouts durationDRYBOUTS duration, WETBOUTSNB wet bouts number and dry bouts numberDRYBOUTSNB numbers) we used generalized linear mixed-effects model. ~~Months elapsed since departure (the duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on), month of the year (i.e. January and so on), sex, and stage (only for i)) were included as fixed effects.~~, and random slopes and intercept to allow activity parameters to randomly vary between individual and time elapsed since departure (Zuur 2009a)~~. ~~We also added tThe use of ii~~To test for the importance of individual variability in our results we built models with or without random effects~~ndividual identity as a random effect permit to account for pseudo-replication issues, since the same individual provided several values~~. We compared models without random effect, models with random intercepts, and models with random slopes and intercepts to test whether the rate of change of activity parameters as a function of time elapsed since departure varied between individuals (Zuur 2009a). Models included month elapsed since departure as a continuous covariate~~fixed factors~~ modelled with non-parametric smoothing functions (Wood 2017). We limited the amount of smoothing (k) with the 'gam.check' function following Wood (2017) for each spline to avoid excessive flexibility and model overfitting that would have no ecological meaning. ~~Month elapsed since departure and month of the year were used to test for time variation in activity parameters. We considered the number of months elapsed since departure available for all individuals (28 months since departure for juveniles and 9 months since departure for immatures and adults). Thus, for all stages combined we considered the lowest number of months elapsed since departure available (9 months since departure). We first ran models testing for variability in PROPWATER, WETBOUTS, DRYBOUTS, WETBOUTSNB and DRYBOUTSNB independently for each stage (juvenile, immature and adult) and then by combining all stages (see Supplementary B; Table S2).~~

~~Models investigating the causes of variability of PROPWATER (GLMM 1 to 4, Table S2) were fitted using the package MASS and nlme and the function "*lme*" (Zuur 2009; Pinheiro et al. 2013). Response variables were visually tested for normality (through Q-Q plots) and homoscedasticity (using Cleveland dotplots; (Zuur et al. 2010) before each statistical test. The error structure approached the normal distribution, and therefore a Gaussian family (link = "identity") was selected for all models.~~

~~Models investigating the causes of variability of WETBOUTSNB and DRYBOUTSNB (GLMM 9 to 16, Table S2) were fitted using the MASS, lme4 packages and the function "*glmer*" (Zuur 2009; Pinheiro et al. 2013; Bates et al. 2014) with a Poisson distribution. Models validation was done following Zuur et al. (2009).~~

Models ~~for PROPWATER, WETBOUTSNB and DRYBOUTSNB~~ including all combinations of explanatory variables and random effects were then tested and ranked using their Akaike Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach (Burnham and Anderson 2002). The model with the lowest AIC was considered as the best model. Two models separated by a difference in AIC values of less than 2 were assumed to fit the data similarly.

~~Models investigating the causes of variability of WETBOUTS and DRYBOUTS (glmmPQL 1 to 8, Table S2) were fitted using the function "fitdist" from the package DHARMa to assess the fit of residuals to a Gamma distribution. In this case, we fitted final models with penalized quasi-likelihood using the glmmPQL function in the package MASS (Venables and Ripley 2002). This meant that model simplification could proceed only on the basis of marginal Wald t tests produced in the model summary ((Bolker et al. 2009)Table S7a). We therefore refitted models without interactions (i.e. sex * month.elapsed for models for juveniles), until all remaining terms were significant ((Crawley 2012)for models specifications and sample sizes see Supplementary material Appendix 1, Table S7b).~~

~~Multi-collinearity among covariates was assessed using variance inflation factors (GVIFs, *AEDForecasting* library in R (Zuur 2009)) and a cut-off value of 3 was used to remove collinear variables prior to modeling.~~

Variation in body size ~~with sex~~

Differences between sexes in body size measurements were tested using Student's t-tests and Wilcoxon rank tests ~~(see Supplementary A)~~. We tested independently if each ~~body~~ measurements (wing length, tarsus length, bill length, bill depth and body mass) varied according to sex and stage (juvenile and adult). The effects were tested using generalised linear models (GLMs) with a Gaussian family and identity link function (Zuur 2009b). Model validation and model selection were performed following (Zuur 2009b). Although sexes and stages differed for some body size measurements, we could not include body size as an additional explanatory variable in GAMMs testing for factors of variation in activity patterns due to small sample sizes in each sex and stage category, and due to unbalanced sampling.

Spatial and statistical analyses were performed using (R Core Team 2021). Values are means ± SD.

Results

Changes in a~~A~~ctivity ~~parameters~~ for all~~between~~ stages

The most parsimonious models ~~(i.e. lowest AICc)~~ explaining variations in activity parameters in Amsterdam albatross included ~~time (~~time elapsed since departure from the colony, ~~and~~ month of the year~~)~~, stages and sexes (Table 3; Supplementary Figures S1 - S5; Tables S2 and S3), whatever the synthetic activity variables~~gradients~~ considered (PC1S, PC2S and PC3S). Selected models also included random effects on intercepts and slopes, indicating inter-individual variability in activity and inter-individual variability in the rate of change of activity as a function of time elapsed since departure from the colony. ~~The three synthetic activity covariates (PC1S, PC2S, PC3S) varied significantly with stage and sex(Supplementary Figures S1 - S5; Tables S2 and S3).~~ Compared to adults, immatures and even more so juveniles, ~~tended to~~ spent a lower percentage of time on water (Table 4, Supplementary Figures S1) and ~~to~~ mad~~k~~e more flying bouts (PC1S; Supplementary Figures S2), made shorter and fewer bouts on water (PC2S; Supplementary Figures S4-S5), and made longer flying bouts (PC3S; Supplementary Figures S2). Males ~~tended to~~ spent~~d~~ a higher percentage of time on water and ~~to~~ mad~~k~~e fewer flying bouts (PC1S), longer and more numerous bouts on water (PC2S) and shorter flying bouts (PC3S) compared to females. The two synthetic activity variables~~covariates~~ (PC1S, PC2S) also varied significantly with time exhibiting clear nonlinear temporal patterns (Figure 1). These variations were related to the time elapsed since their departure from the colony and showed seasonal changes (indicated by the month of the year; Supplementary Figures S1 - S5; Tables S2 and S3). With increasing time since departure ~~The~~ birds ~~tended to~~ spent~~d~~ lower percentage of time on water and made shorter wet bouts~~, but made longer dry bouts~~. They~~to~~ spent less percentage of time on water ~~make more flying bouts~~ during the period March to July compared to rest of the year (PC1S, Supplementary Figures S1 - S5). They made~~. The seasonal change is also observed through~~ longer and fewer bouts ~~spent~~ on water during the period April to November, and shorter flying bouts during the period ~~Septem~~November to ~~December~~February~~at the end of the year (PC2S: September-December; PC3S: October-December)~~. ~~Finally, j~~Juveniles showed strong and abrupt temporal changes in ac~~i~~tivity linked to the time elapsed since departure from the colony~~, in other words their behaviour changed~~ in the first two months after fledging (Supplementary Figure S6). In immatures and ~~in~~ adults the temporal pattern appeared reversed compared to juveniles (Supplementary Figure S6).

Changes in a~~A~~ctivity of~~parameters in~~ juveniles during~~in~~ the first two years after fledging

In juveniles Amsterdam albatross, the most parsimonious models explaining variations in activity ~~parameters~~ included ~~time (~~time elapsed since departure from the colony,~~ and~~ month of the year~~)~~ whatever the activity variables~~gradients~~ considered (Table 5; PC1J, PC2J and PC3J), and sexes~~es~~ (PC2J and PC3J). Selected models also included random effects on intercepts and slopes, indicating inter-individual variability in activity and inter-individual variability in the rate of change of activity as a function of time elapsed since departure from the colony (S~~Table X~~upplementary Figures S7).

~~The second and third covariates (~~PC2J and PC3J~~)~~ varied significantly with sex (Supplementary Figures S8 - S11; Tables S5b, 5c), indicating that juvenile males ~~tended to~~ mad~~k~~e shorter and more numerous bouts on water (PC2J) and shorter flying bouts (PC3J) compared to females (Supplementary Figures S8 - S11; Tables S5b, 5c). ~~The first two activity covariates (~~PC1J and PC2J~~) also~~ varied significantly with time exhibiting clear nonlinear temporal patterns (Figure 2~~). These variations were related to the time elapsed~~

~~since their departure from the colony and showed seasonal changes (indicated by the month of the year;~~ Supplementary Figures S8 - S12; Tables S2 and S4a, 4b). Juveniles~~The birds~~ seemed to alternate periods of lower percentage of time spent on water combined with more numerous flying bouts (April) with periods of higher percentage of time on water combined with fewer flying bouts (February, July-October; PC1J~~S~~, not illustrated). The seasonal change was~~is~~ also observed through longer and fewer bouts spent on water and shorter flying bouts at the end of the year (PC2J~~S~~: September-December~~J~~). ~~Finally, j~~Juveniles ~~showed temporal changes in their behaviour linked to the time elapsed since departure from the colony (Figure 2). In other words~~, during the first 28 months after fledging, ~~they tended to~~ increased the time spent on water while decreasing the number of flying bouts (Figure 2a). ~~TheshipPC2Jsince departure wasindicating wet bout duration~~

~~Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and bill depth whatever the stage (juvenile or adult; see Supplementary A Table S2-S7). In juveniles, males were ~13% heavier than females, while the difference was not significant in adults. The most sexually dimorphic phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they were body mass, tarsus length and bill length.~~

~~All stages exhibited clear temporal patterns in their activities, related to the time elapsed since their departure from the colony and showing seasonal changes (indicated by the month of the year) whatever the five activity metrics considered (Figures 1-5; Supplementary B Tables S2-S7d). Juveniles showed strong temporal changes linked to the time elapsed since departure from the colony (Figure 1). From the first month since departure, there was a quick decrease in the proportion of time spent on sea surface (mean value for the 1st month: 73.4±16.1%, for the 3rd month: 47.2±18.3%), in the duration of bouts on water (mean duration for the 1st month: 1.21±1.93h, for the 6th month: 0.99±1.42h) and in the numbers of bouts on water (mean number for the 1st month: 11.34±4.96, for the 3rd month: 7.43±3.59), but an increase in the duration of bouts flying (mean duration for the 1st month: 0.89±0.97h, for the 3rd month:~~

~~1.38±1.45h), and the numbers of bouts flying (mean number for the 1st month: 6.18±3.14, for the 3rd month: 7.86±3.11). Although less pronounced, the activity (proportion of time spent on seawater, the duration of bouts on water and the numbers of bouts on water or flying; Supplementary B Tables S2) also varied according to the month of the year with two distinct periods (from November to February-March and from April-May to October). Highest values in the proportion of time spent on seawater, duration of bouts on water and numbers of bouts flying tended to be observed from November to February-March (Figure 1; Supplementary B Table S3a). In immatures and in adults the temporal pattern, i.e. months since their departure from the colony, of the activity parameters appeared generally reversed compared to juveniles (Figures 1-5; Supplementary B Tables S2, S3a-d, S4a-d, S5a-d, S6a-d, S7a-d). For the proportion of time spent on sea surface, the duration and the number of bouts on water, values were low early after departure then increased during the following months to peak ~ 3-5 months later, and finally tended to decrease at the end of the period. The opposite pattern was observed for duration and number of bouts flying. Regarding the seasonal changes (i.e. months of the year; Figures 1-5; Supplementary B Tables S2, S3a-S7d), for immatures, the temporal pattern tended to differ for all activity parameters when compared to that of months elapsed since departure. This was not the case for adults which exhibited alike temporal patterns. Furthermore, temporal patterns varied differently by sex whatever the stage considered (Figures 2-5; Table 3).~~

~~When taking into account all three stages (juveniles, immatures and adults), interactions between the variables months elapsed since departure and stage, and between month of the year and stage were highly significant when explaining all the parameters of activity (proportion of time spent on seawater, the duration of bouts on water or flying and the numbers of bouts on water or flying; Supplementary B Tables S2). Therefore the difference between on one hand juveniles, and on the other hand immatures and adults depended on the number of months spent at sea since departure from the colony but also on~~

~~the month of the year (Figures 1-5). Juveniles had very contrasted temporal patterns for all the activity parameters and almost never reached values of activity parameters observed for immatures and adults (Tables 4, Supplementary B Tables S3d, S4d, S5d, S6d, S7d, Figures S1-S4). This was all the more pronounced when considering the time spent on sea surface (Figure 1), the duration (Figure 4) or the numbers of bouts on water (Figure 5), and the numbers of flying bouts (Figure 3). Juveniles spent more time in flight, with more frequent bouts as early as the second to third months spent at sea after their departure. During the 9 first months spent at sea after departure all the activity parameters of juveniles differed in values and in patterns when compared to immatures or adults.~~

~~When comparing all three stages (juveniles, immatures and adults), interactions between the number of months elapsed and sex, and between month of the year and sex were highly significant when explaining almost all activity parameters (Appendix A Table S2).~~

~~In juveniles, during the first 28 months spent at sea (after departure), there was a significant effect of the time elapsed (months), the month of the year and the sex for all activity parameters considered except for the proportion of time spent on seawater (Table 3, Appendix A Tables S2, S3a, S4a, S5a, S6a, S7a, Figures 2-6). In juveniles, males tended to spend more time sitting on water (higher wet bouts duration) and more frequently (higher wet bouts numbers; Figures 4-5, Appendix A Figures S1-S4) than females. Nonetheless, these differences varied according to the time elapsed and with the month of the year. The time spent on the water by juveniles changed during the first 28 months at sea (Figure 6). While it decreased rapidly during the first two months after fledging, it remained low (47-52%) during the next 14 months and then increased again. Interestingly, the same pattern as the one observed in immature and adult birds was found with a 15-16 months of delay in juveniles, reaching similar values (Figure 6).~~

~~In immatures, males tended to spend more time sitting on water (higher time spent on water and wet bouts duration) but less frequently (lower wet bouts numbers; Table 3, Appendix A Tables S2, S3b, S4b, Figures 4- 5) than females. Conversely, in juveniles and adults there was no significant effect of sex on the proportion of time spent on the water (Tables 4, Appendix A Table S2).~~

~~In adults, males tended to spend less time flying (lower dry bouts duration) and flied less frequently (lower dry bouts numbers; Table 3, Appendix A Tables S4c, S5c, S6c, S7c; Figures 2- 3) than females, but there was no significant effect of sex on the proportion of time spent on the water (Appendix A Tables S2, S3c).~~

~~Depending on the activity parameters considered the difference between adult males and adult females appeared at different timing of the year (month of the year) and of their journey (months elapsed since departure; Figures 2-5, Appendix A Tables S4c, S5c, S6c, S7c). Occasionally these differences were more pronounced early after departure from the colony during the first four months (dry bouts duration; Figure 2) or during the next few months (wet bouts duration-figure 4 and dry bouts number-Figure 3).~~

Body size

Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and bill depth whatever the stage (juvenile or adult; Tables 6-12). In juveniles, males were ~13% heavier than females, while the difference was not significant in adults (Table 6). The most sexually dimorphic phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they were body mass, tarsus length and bill length.

Discussion

Using miniaturized activity loggers (GLS), we showed ~~a~~ clear differences and changes in activity characteristics depending on life-stages, time and~~or~~ sex. ~~Elucidating the transition to independence in early life stages is crucial for understanding the causes of higher juvenile mortality in long-lived species (Fay et al. 2015; Payo-Payo et al. 2016).~~ By comparing changes in behaviour at sea and foraging parameters of juveniles ~~up to 28 months~~ after their departure at sea with those of immatures and adults in the Amsterdam albatross, we showed that juveniles differed from immatures and adults in their activity values and patterns. In this study, we benefited from a unique comprehensive dataset of remarkable duration (up to 28 months) to characterise the post-fledging behaviour of naïve seabirds. Although one limitation of our study was that individual longitudinal data were not long enough to explore changes in behaviour from fledging to the adult stage, t~~T~~hese results provide new insights into the timing and the change of behaviour in naïve individuals over a unique dataset in a long-lived endangered seabird species. ~~One of the limitations of our study is that no sufficient long individual longitudinal data exist to explore the change of behaviour from fledging to the adult stage.~~.

Stage specific changes

The birds were found to behave differently according to their stage whatever the activity variables~~gradients covariates~~ considered, indicating differences in foraging behaviour. Overall,~~Globally~~ juveniles ~~tended to~~ spent~~d~~ lower percentage of time on water compared to immatures and adults. Nonetheless, ~~D~~during the first month following their departure from the colony while ~~juveniles~~ the proportion of time spent on water by ~~the~~ immatures and ~~the~~ adults showed a ~~typical~~ dome-shaped curve peaking~~with a maximum~~ three to five months after ~~their~~ departure, ~~the~~ juveniles ~~spent a greater~~changed abruptly ~~proportion of time sitting on water~~, with values dropping off in the first two months and then remaining low and overall lower than in adults and immatures~~did longer and more numerous bouts on water, and shorter and less numerous flying bouts than immatures and adults~~. This might indicate a lower foraging activity~~effort~~ in naïve birds. During the same period, the ~~gradient~~ duration and~~-~~ number of water bouts also exhibited ~~also~~ progressive change~~, but nonlinear trend with the lowest duration reached by mi-period~~. T~~However, from the second month following departure from the colony t~~he~~i~~se patterns suggest~~ed~~ an early and gradual change in foraging behaviour ~~reversed and the~~and ~~suggested~~ that juveniles progressively behaved similarly to immatures and adults (reaching similar values in activity covariates)~~activity patterns of juveniles became similar to that of immatures and adults~~. It is noteworthy that the multi-monthly bell~~dome~~-shaped pattern observed during the first 10 months after departure in immatures and adults appears to be mirrored in juveniles 15-16 months later (see Figure S12). ~~only 10 to 17 months after fledging depending on the activity parameter considered (see Figure 6).~~ Together, these results suggest a progressive behavioural change~~s~~ ~~improvement of~~ in movements ~~performances~~ during the first two months after~~since~~ fledging. ~~Juvenile naïve birds during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, higher duration and more numerous bouts on water, and lower duration and less numerous flying bouts). They reach values similar to those of immatures and adults 2 to 3 months after departure (except for the number of dry/wet bouts for which it took longer), suggesting a progressive improvement of foraging performances during the first two months since fledging.~~ This ~~suggests~~ seems to indicate that juvenile individuals ~~are therefore very likely to~~may have ~~poorer~~ weaker foraging skills during their first two months ~~spent~~ at sea. Although behavioural changes can often equate to improved performance (e.g. ~~(~~Campioni et al. 2020) this is not always the case. The emergence of juvenile birds as more '*adult like*' in their foraging/flight behavioural patterns is not necessarily a sign of improvement.

~~Characteristics of immatures and adults~~Results suggest that immatures may differ from both adults and juveniles in some aspects of their behaviour. While most of the activity parameters and the temporal patterns showed similarities with adults when considering the time elapsed since departure, they seemed rather comparable to juveniles when considering seasonal aspects (month of the year). Such inconsistency can be explained by several non-exclusive explanations: i) similar management of energy constraints than adults, as post-breeding~~er~~ adults and immatures are less constrained in their central-place foraging strategies (Campioni et al. 2016), ii) comparable capacity to respond to local resource availability in their foraging behaviour than juveniles (Frankish et al. 2022), and iii) incomplete acquisition of more long-term learning of complex movement strategies (Thorup et al. 2003; Votier et al. 2011; Rotics et al. 2016). Disentangling among these hypotheses~~ement~~ can be achieved by combining higher resolution movement data with longer longitudinal studies~~y~~ covering all three life stages for same individuals. ~~Elucidating the transition to independence in early life stages is crucial for understanding the causes of higher juvenile mortality in long-lived species (Fay et al. 2015; Payo-Payo et al. 2016).~~Since all stages of the Amsterdam albatross forage in the same water masses (see Thiebot et al. 2014), differences in foraging behaviour were presumably not due to different oceanographic characteristics as observed in other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al. 2020b). These lower performances could be due to a combination of lack of experience of optimal behaviours, poor knowledge of the environment, use of distinct cues and/or physical immaturity (Shaffer et al. 2001; Frankish et al. 2020a, 2022). It is likely that increasing exposure to diverse foraging situations allows juveniles to rapidly accumulate foraging experience and improve various aspects of foraging.

What might be designated as ~~The~~ '*lower performance*' of juveniles ~~we~~ found in our study is consistent with studies on wandering albatrosses and Amsterdam albatrosses (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2017; Pajot et al. 2021) during the first weeks at sea.~~,~~ F~~f~~ledging juvenile albatrosses behaved differently and ~~which found~~ that shortly after ~~fledging juvenile albatrosses~~they employ similar foraging strategies as adults (Frankish et al. 2022). Additional skills (such as detection of prey at the surface, detection of other foraging seabirds, navigational skills…) need to be acquired during the immature period before the efficiency of these behaviors matches that of adults. This is also typical of other seabird taxa, which show progressive improvement in flight performance with the numbers of days since fledging (Yoda et al. 2004; Mendez et al. 2017; Collet et al. 2020; Corbeau et al. 2020; Frankish et al. 2022). For example juvenile brown boobies *Anous stolidus* improved their flight abilities (Yoda et al. 2004) and juvenile European shags *Phalacrocorax aristotelis* compensate for poor foraging success by increasing their foraging time during first months after fledging (Daunt et al. 2007). In contrast, flight capability (flight

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speed and sinuosity) comparable to that of adults allows juvenile white-chinned petrels *Procellaria aequinoctialis* to rapidly flew large distances from the colony (Frankish et al. 2020).

Notwithstanding the progressive ~~improvement~~ change of movement ~~performances~~ behaviours (foraging parameters estimated from activity parameters improved with time elapsed) quantified in juvenile Amsterdam albatrosses, it remains elusive whether this is a question of physical development and/or a matter of gaining experience. Elucidating the transition to independence in early life stages is crucial for understanding the causes of higher juvenile mortality in long-lived species (Fay et al. 2015; Payo-Payo et al. 2016).

~~Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013; Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by differences in foraging habitats. We found support for the body size hypothesis to explain sex differences in activity parameters (except for the time spent on water), consistent with the important sexual dimorphism in the Amsterdam albatross. Males tended to spend more time sitting on water (wet bouts duration) whatever the stage, and depending on stage more (for juveniles) or less (for immatures and adults) frequently compared to females. Consistently, we found that males tended to fly for shorter periods (dry bouts duration) compared to what females did and possibly less frequently (dry bouts number) depending on time. Whatever the stage, there was no significant effect of sex on the proportion of time spent on the water (except in immatures where males tended to spent more time sitting on water compared to females).~~

~~Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the Wandering albatross, although subtle differences can appear (Pajot et al. 2021).(Delord et al. 2013) Although Amsterdam albatross is 5-8%~~

~~smaller and 25% lighter than wandering albatross, the two species have a very close anatomy and similar use of the wind. In the wandering albatross, due to sex differences in flight performance, specifically, due to their higher wing loading, males should both maintain longer flying effort and be more likely to minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). Hence, wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997b). However, this strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a more important utilization of the '*sit-and-wait*' technique and possibly to vary depending on sites suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the former technique (compared to '*foraging-in-flight*'). In other word, males may have more of a '*sit-and-wait*' strategy while females have more of a '*foraging-in-flight*' strategy, although there is some behavioural plasticity particularly over time. Our prediction that foraging behaviour differs between sexes was fully supported (i.e. sex-differences in bouts duration and number). Nevertheless, the similarity in time spent on the water suggests that the differences may be more subtle, showing some a trade-offs in duration and numbers between flying and water bouts. This trade-off should vary depending on stage as immature females tended to have shorter and more frequent bouts on the water. This implies that while probably feeding on similar water masses, the sexes might differ in type of prey targeted and/or used different foraging methods. The confirmation of this hypothesis reinforces the fact that the two-sibling species, as previously assumed, show a high degree of similarity in their foraging behaviour.~~

~~Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey~~

~~(Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019; Barbraud et al. 2019). It has also been suggested that size matters probably because the smaller and lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower wing loaded female wandering albatrosses, compared to males, are probably better able to exploit subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al. (2002); Stauss et al. (2012)).~~

Temporal changes in activity

The temporal variability of activity was found whatever the life-stage considered. Part of the activity changes observed following the departure of juveniles Amsterdam albatross may illustrate the swift change in travel and movement behaviour, reflecting a more '*adult like*' behaving, not indicating necessarily an improvement of flight performances and of the ability to cope with changing (i.e. increasing wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such as albatrosses. Both extrinsic (i.e. environmental conditions: variability in subtropical waters resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew) factors could be involved in the modulation of foraging behaviour, which can be reflected in the temporal variability~~ of activity parameters we found whatever the stage~~. Subtropical environments in the southern Indian Ocean are generally characterized as oligotrophic areas but nonetheless are known to vary over the seasons. During the austral winter, colder surface waters and strong winds result in changes of oceanographic conditions associated with an increased primary productivity (Behera and Yamagata 2001; Terray 2011; Delord et al. 2021). Changes in water temperature associated with wind appear to result in seasonal biological production variations that affect seabirds (Delord et al. 2021).~~, however, the delay between the increase in primary production and~~

~~the increase in potential prey for albatrosses is probably rather long in this oligotrophic context. These changes were found to affect seabirds (Delord et al. 2021). Part of the activity changes observed following the departure of juveniles Amsterdam albatross could reflect improvement of flight performances and of the ability to cope with changing (i.e. increasing wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such albatrosses.~~

In seabirds,

~~T~~temporal changes in foraging activities ~~were~~ are often associated to the very strong contrast between reproduction and inter-breeding periods, shifting from high energetic needs linked to reproductive effort and associated constraints (i.e. central place foraging strategy; ~~(~~Orians and Pearson 1979~~)~~) to a reduction of these energetic constraints during the non-breeding period (sabbatical year for adults) (Williams 1966; Ricklefs 1977, 1983; Stearns 1992; Ydenberg et al. 1992). This contrast is particularly pronounced in seabirds (Mackley et al. 2010; Gutowsky et al. 2014) where energetic constraints play a decisive role in determining activity patterns (Phalan et al. 2007).

Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). ~~In large-sized albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch 1991).~~ Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting important constraints ~~that could compete with breeding (immature birds tend to renew fewer feathers compared to adult breeders), and particularly in females~~ (Weimerskirch 1991; see Supplementary). ~~In smaller sized seabirds, a link between moulting pattern and activity parameters was evidenced, resulting in a clear temporal pattern partly explained by moult (Cherel et al. 2016).~~ Recently Gutowsky et al. (2014)

suggested that tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could compromise flight from active wing moult during the non-breeding period and induce changes in daily activity budget during a 'quasi-flightless' stage. However, there is no such data for southern albatrosses. Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested it such a compromise. However, adult birds during the non-breeding season appear to spend much more time on the water during winter, suggesting that partial moult may occur at this time, as observed in many other seabird species that have to moult during the non-breeding season and show reduced activity during specific periods that may correspond to moulting (Weimerskirch et al. 2015b, 2020). Interestingly, immature appear to have this peak in time spent on the water in spring, suggesting different timing of moult.

Sex differences in activity

Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013; Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by differences in foraging habitats. We found support for the body-size hypothesis to explain sex differences in activity parameters, consistent with the important sexual dimorphism in the Amsterdam albatross. Males did~~tended to spend~~ more ~~numerous~~ bouts on water whatever the stage, and depending on stage, shorter (juveniles only) compared to females. Consistently, we found that males flew~~tended to fly~~ for longer periods (dry bouts duration) compared to ~~what~~ females ~~did~~. When considering all stages, males spent a higher percentage of time on water compared to females.

Amsterdam albatross and its sister species the wandering albatross have a very close anatomy and similar use of the wind, although Amsterdam albatross is 5-8% smaller and 25% lighter (Barbraud et al. unpublished data. In the wandering albatross, due to sex differences in flight performance (specifically, due to their higher wing loading), males should both maintain longer flying effort and be more likely to minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). The change in foraging strategy, as in wandering albatross, tends to be dependent on breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a greater use of the '*sit-and-wait*' technique and may vary between sites, suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the '*sit-and-wait*' technique (compared to '*foraging-in-flight*'). In other word, males may have more of a '*sit-and-wait*' strategy while females have more of a '*foraging-in-flight*' strategy, although there is some behavioural plasticity particularly over time. Our prediction that foraging behaviour differs between sexes was fully supported (i.e. sex-differences in activity parameters). Nevertheless, the similarity in time spent on the water suggests that the differences may be more subtle, showing some a trade-offs in duration and numbers between flying and water bouts. This trade-off should vary depending on stage as immature females tended to have shorter and more frequent bouts on the water. This implies that while probably feeding on similar water masses, the sexes might differ in type of prey targeted and/or used different foraging methods. The confirmation of this hypothesis reinforces the fact that the two-sibling species, as previously assumed, show a high degree of similarity in their foraging behaviour.

Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey (Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019; Barbraud et al. 2021). It has also been suggested that size matters probably because the smaller and lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower wing loaded female wandering albatrosses, compared to males, are probably better able to exploit subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al. (2002); Stauss et al. (2012)).

Individual variability in activity

There was inter-individual variability in almost all activity parameters whatever the stage considered. In juveniles, models indicated inter-individual variability in activity and in the rate of change of activity as a function of time elapsed since departure from the colony. Since the intercept terms in the models were significant, it seems as though individual variability (i.e., specialization on different foraging strategies) was a contributor to observed variability. However, the rate of change of intra-individual variation for some foraging strategies (percentage of time on water-number of flying bouts axis) oscillated during the juvenile period with a seemingly remarkable synchrony (see Fig S7). This suggests that changes in foraging behaviours occurred at the individual level during the juvenile period without stabilizing, at least during the first two years after fledging. This individual variability suggests development of specialized individual foraging behaviours (Harel et al. 2016; Rotics et al. 2016, 2021; Phillips et al. 2017). Nonetheless, given the small sample sizes these results should be interpreted with caution.

Conclusion

Very few studies have investigated the ontogeny of foraging behaviour over such a long period of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over several years. We investigated the foraging behaviour, through activity patterns, during the three life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naïve juveniles, immatures and adults. Naïve juveniles during their first month at sea after leaving their colony exhibited lower foraging activity~~effort~~ (greater proportion of time spent sitting on water, longer and more

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numerous bouts on water, and shorter and fewer flying bouts). Patterns of activity parameters in juveniles after independence suggested a progressive change of foraging performances during the first two months since fledging. Regardless of life stage considered, activity parameters exhibited temporal variability reflecting the modulation of foraging behaviour presumably~~. This variability is discussed (~~ linked to both extrinsic (i.e. environmental conditions such as variability in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew during moult) factors~~)~~. S~~We found s~~ex differences in activity parameters according to time ~~(month elapsed ~~since departure from the colony and season~~month of the year),~~ were consistent with the ~~important ~~sexual dimorphism in the Amsterdam albatross. It is therefore expected that a change in behaviour, resulting from the experience gained, may reflect an improvement in skills~~,~~ occurring during a period of learning through the immaturity phase.

Acknowledgements

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Table 1 Chronological characteristics of life-cycle stages of Amsterdam albatross (adapted from Thiebot et al. 2014)

Stage[1]	Definition	Age[1]	Tracking duration	Behaviour
Juvenile	Following chick fledging in January	1st year	~2.5 years	Chicks disperse at sea after leaving the colony for the first time
Immature	After juvenile dispersal, until first breeding attempt (at 9 year old on average)	~2-10 years	~1 year	Non-breeding young birds forage at sea and occasionally visit the colony for mating
Adult sabbatical	Between two successive breeding periods (~ 15 January year *t* to the following 15 January year *t+1*)	~8-28 years	~1 year	Breeding adults at the end of reproductive cycle and leave the colony to forage at sea

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[1] Stage/Age at which the individuals were equipped with loggers in our study

Table 2 Sample sizes of birds tracked using Global Location Sensing (GLS) of Amsterdam albatross

Stage	Years of deployment	Deployed (n)	Recovered (n)	Recovery rate (%)	GLS with data (n)
Juvenile	2011	21	12	57 (t+9)	10 (4 F - 6 M)[1]
Immature	2011-2012	18	17	94	13 (3 F - 9 M – 1 NK)
Adult sabbatical	2006, 2009	11	11	100	10 (6 F - 4 M)

[1] number of females F and males M, or not known NK for each stage

Table 3 Model selection for~~establishing~~ variations in activity parameters of Amsterdam albatrosses in relation to sex, stage, number of months spent since departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on)

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1S)				
M_0	Null model		28874.42	0
M_1	Month elapsed	Month elapsed: Individual	27311.97	1562.45
M_2	Month elapsed + Month	Month elapsed: Individual	26968.28	1906.14
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	26889.23	1985.19
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	26852.86	2021.56
Bouts spent on water (PC2S)				
M_0	Null model		26903.12	0
M_1	Month elapsed	Month elapsed: Individual	25803.80	1099.32
M_2	Month elapsed + Month	Month elapsed: Individual	25756.37	1146.75
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	25751.47	1151.65
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	25752.62	1150.50
Bouts spent dry -flying (PC3S)				
M_0	Null model		23042.26	0

Mis en forme : Largeur : 27,94 cm, Hauteur : 21,59 cm

Tableau mis en forme

Mis en forme : Police :(Par défaut) Calibri, Couleur de police : Noir, Anglais (États-Unis)

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Mis en forme : Police :(Par défaut) Calibri

Tableau mis en forme

M_1	Null model	Month elapsed: Individual	22540.25	502.01
M_2	Month elapsed	Month elapsed: Individual	22539.75	502.51
M_3	Month	Month elapsed: Individual	22509.79	532.47
M_4	Month + Stage + Sex	Month elapsed: Individual	22427.29	614.97

Models are ranked according to decreasing statistical support, as indicated by AICc. The first best models are shown

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Mis en forme : Police :(Par défaut) Calibri

Table 4 Values of activity parameters (mean ± sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam albatross

	Juvenile[1]		Juvenile[2]		Immature		Adult sabbatical	
	female	male	female	male	female	male	female	male
Time spent on water (%)	55.04 ± 20.46	58.18 ± 21.11	51.41 ± 19.18	52.88 ± 20.39	59.25 ± 21.53	63.31 ± 21.17	64.89 ± 20.90	69.98 ± 18.10
Wet bouts (sitting on water) duration (h)	1.21 ± 1.74	1.24 ± 1.76	1.16 ± 1.73	1.12 ± 1.59	1.07 ± 1.31	1.48 ± 2.12	1.47 ± 1.95	1.33 ± 1.96
Dry bouts duration (h)	1.29 ± 1.37	1.21 ± 1.32	1.34 ± 1.41	1.26 ± 1.40	1.32 ± 1.42	1.28 ± 1.55	1.44 ± 1.56	1.31 ± 1.42
Wet bouts (sitting on water) number	8.71 ± 4.01	8.76 ± 4.09	8.14 ± 3.85	8.48 ± 4.11	10.34 ± 4.29	8.59 ± 4.24	8.96 ± 3.98	10.28 ± 5.33
Dry bouts number	7.06 ± 3.20	7.27 ± 3.52	7.57 ± 3.21	7.85 ± 3.50	6.31 ± 3.21	5.75 ± 2.99	5.01 ± 2.64	4.64 ± 2.48

[1] calculated during 28 months following departure; [2] calculated during 9 months following departure

Table 5 Model selection for~~establishing~~ variations activity parameters for juveniles Amsterdam albatrosses in relation to sex, number of months spent since departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on)

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1J)				
M_0	Null model		22109.52	0
M_1	Month elapsed	Month elapsed: Individual	21864.11	245.41
M_2	Month elapsed + Month	Month elapsed: Individual	21625.69	483.83
Bouts spent on water (PC2J)				
M_0	Null model		20417.76	0
M_1	Month elapsed	Month elapsed: Individual	20072.42	345.34
M_2	Month elapsed + Month	Month elapsed: Individual	20004.65	413.11
M_3	Month elapsed + Month + Sex	Month elapsed: Individual	19999.00	418.76
Bouts spent dry -flying (PC3J)				
M_0	Null model		17708.47	0
M_1	Null model	Month elapsed: Individual	17548.75	159.72
M_2	Month elapsed	Month elapsed: Individual	17549.00	159.47
M_3	Month + Sex	Month elapsed: Individual	17541.02	167.45

Mis en forme : Largeur : 27,94 cm, Hauteur : 21,59 cm

Tableau mis en forme

Mis en forme : Couleur de police : Noir

Mis en forme : Couleur de police : Noir

Models are ranked according to decreasing statistical support, as indicated by AICc. The first best models are shown

Table 6 Body measurements of juveniles and adults Amsterdam albatross and percentage of differences between sexes for each measurement. Δ is the difference in %, p values are reported

	Juvenile		Adult		Δ		Dimorphism ratio[1]		t-test[2]	
	Female (n=159)	Male (n=162)	Female (n=30)	Male (n=45)	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
Wing length (mm)	532.3 ± 62.1	543.6 ± 72.5	637.0 ± 13.3	654.7 ± 14.7	2.1	2.7	1.021	1.026	**W=10554** **P<0.01**	**t_{64}=-4.882** **p<0.001**
Tarsus length (mm)	113.1 ± 3.8	118.4 ± 3.8	112.4 ± 3.9	116.4 ± 4.0	4.5	3.5	1.047	1.077	**t_{229}= -10.54** **p<0.001**	**t_{28}= -3.982** **p<0.001**
Bill length (mm)	137.1 ± 4.0	143.1 ± 3.8	140.9 ± 4.7	145.0 ± 3.5	4.2	2.8	1.044	1.034	**t_{319}= -13.89** **p<0.001**	**t_{72}= -4.268** **p<0.001**
Bill depth (mm)	34.8 ± 3.4	36.9 ± 3.4	36.0 ± 1.5	38.0 ± 1.5	5.8	5.2	1.061	1.000	**t_{318}= -5.629** **p<0.001**	**t_{58}= -4.821** **p<0.001**
Body mass (g)	7719 ± 1228	8859 ± 1546	7509 ± 1561	7257 ± 1207	12.9	3.4	1.148	1.077	**t_{193}=-5.846** **p<0.001**	t_{32}=0.512 p=0.612

[1] ratio calculated as Male/Female following (Lovich and Gibbons 1992) for species for which males are known to be larger than females cited in (Smith 1999); [2] Student's t-tests used after check for normality of the data for all measurements except for wing length of juveniles (Wilcoxon rank test)

Table 7 Selected generalized linear models testing for the effect of sex and stage on body measurements of Amsterdam albatross

Model #	**Study variable**	**Model**	**Sample size**
GLM1	Wing length	~ sex + stage	387
GLM2	Tarsus length	~ sex + stage	299
GLM3	Bill length	~ sex	395
GLM4	Bill depth	~ sex	380
GLM5	Body mass	~ sex + stage	242

Table 8 GLM results for wing length of Amsterdam albatross modelled as a function of sex and stage (GML1). Reference values are female and adult. The degrees of freedom were 384

	Estimate	Std.Error	t-value	p-value
(Intercept)	638,68	17,43	36,651	p<0.001
Male	16,97	7,28	2,331	p<0.05
Juvenile	-95,24	17,27	-5,516	p<0.001

Table 9 GLM results for tarsus length of Amsterdam albatross modelled as a function of sex and stage (GLM2). Reference values are female and adult. The degrees of freedom were 296

	Estimate	Std.Error	t-value	p-value
(Intercept)	110,54	0,95	116,42	p<0.001
Male	4,92	0,45	11,01	p<0.001
Juvenile	2,56	0,94	2,73	p<0.01

Table 10 GLM results for bill length of Amsterdam albatross modelled as a function of sex (GLM3). Reference values are female. The degrees of freedom were 393

	Estimate	Std.Error	t-value	p-value
(Intercept)	137,65	0,30	462,98	p<0.001
Male	5,88	0,41	14,31	p<0.001

Table 11 GLM results for bill depth of Amsterdam albatross modelled as a function of sex (GLM4). Reference values are female. The degrees of freedom were 378

	Estimate	Std.Error	t-value	p-value
(Intercept)	34,94	0,24	147,74	p<0.001
Male	2,16	0,33	6,60	p<0.001

Table 12 GLM results for body mass of Amsterdam albatross modelled as a function of sex and stage (GLM5). Reference values are female and adult. The degrees of freedom were 239

	Estimate	Std.Error	t-value	p-value
(Intercept)	6777,60	417,10	16,25	p<0.001
Male	911,50	186,20	4,90	p<0.001
Juvenile	958,70	412,80	2,32	p<0.01

~~Table 3 Values of activity parameters (mean ± sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam albatross~~

	~~Juvenile[1]~~		~~Juvenile[2]~~		~~Immature~~		~~Adult sabbatical~~	
	~~female~~	~~male~~	~~female~~	~~male~~	~~female~~	~~male~~	~~female~~	~~male~~
~~Time spent on water (%)~~	~~55.04 ± 20.46~~	~~58.18 ± 21.11~~	~~51.41 ± 19.18~~	~~52.88 ± 20.39~~	~~59.25 ± 21.53~~	~~63.31 ± 21.17~~	~~64.89 ± 20.90~~	~~69.98 ± 18.10~~
~~Wet bouts (sitting on water) duration (h)~~	~~1.21 ± 1.74~~	~~1.24 ± 1.76~~	~~1.16 ± 1.73~~	~~1.12 ± 1.59~~	~~1.07 ± 1.31~~	~~1.48 ± 2.12~~	~~1.47 ± 1.95~~	~~1.33 ± 1.96~~
~~Dry bouts duration (h)~~	~~1.29 ± 1.37~~	~~1.21 ± 1.32~~	~~1.34 ± 1.41~~	~~1.26 ± 1.40~~	~~1.32 ± 1.42~~	~~1.28 ± 1.55~~	~~1.44 ± 1.56~~	~~1.31 ± 1.42~~
~~Wet bouts (sitting on water) number~~	~~8.71 ± 4.01~~	~~8.76 ± 4.09~~	~~8.14 ± 3.85~~	~~8.48 ± 4.11~~	~~10.34 ± 4.29~~	~~8.59 ± 4.24~~	~~8.96 ± 3.98~~	~~10.28 ± 5.33~~
~~Dry bouts number~~	~~7.06 ± 3.20~~	~~7.27 ± 3.52~~	~~7.57 ± 3.21~~	~~7.85 ± 3.50~~	~~6.31 ± 3.21~~	~~5.75 ± 2.99~~	~~5.01 ± 2.64~~	~~4.64 ± 2.48~~

~~[1] calculated during 28 months following departure; [2] calculated during 9 months following departure~~

FIGURES

Figure 1 Modeled a) first and b) second axis of principal components analysis of activity parameters of all stages (i.e. adult, immature and juvenile) of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval.

Figure 2 Modeled a) first and b) second axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval.

~~Figure 1~~

~~Figure 2~~

~~Figure 3~~

~~Figure 4~~

~~Figure 5~~

~~Figure 6~~

Mis en forme : Justifié

Figure 1a

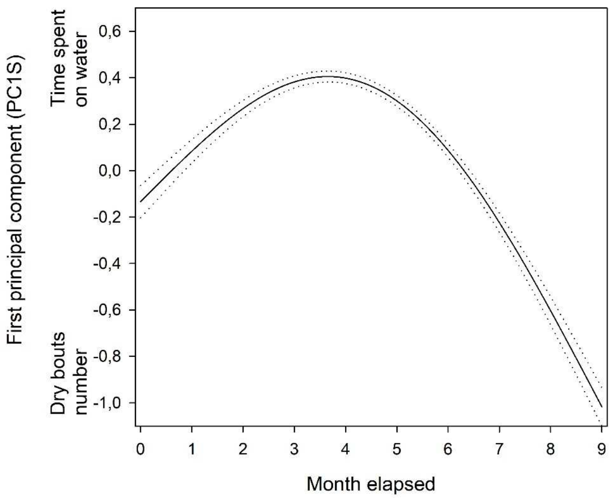
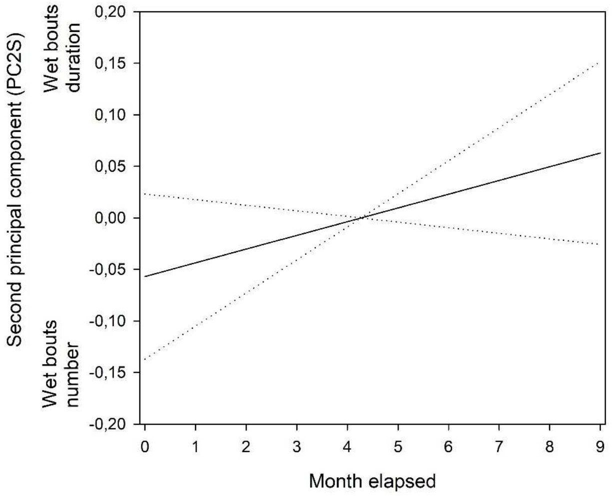


Figure 1b



2423

Figure 2a

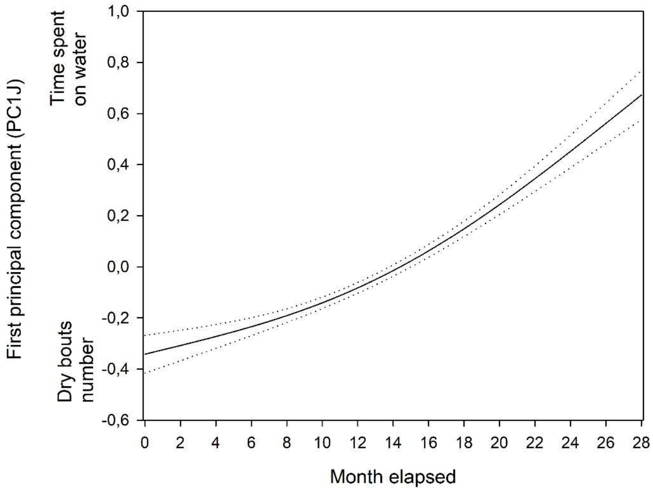
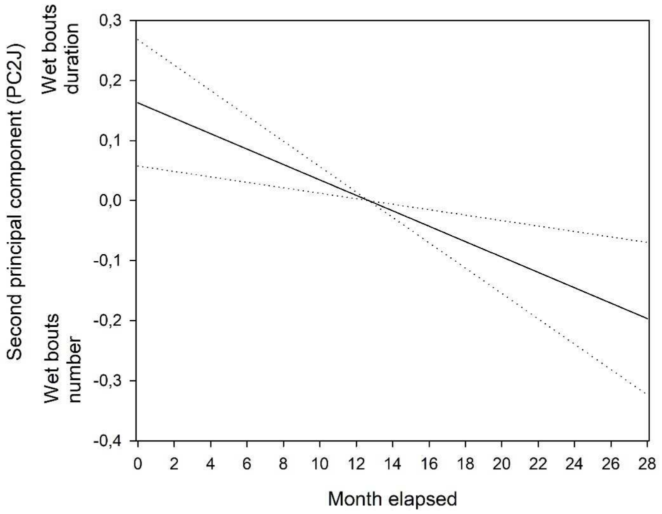


Figure 2b



~~Figure 3~~

~~Figure 4~~

~~Figure 5~~

~~Figure 6~~

The authors of this article declare that they have no financial conflict of interest with the content of this article.

REFERENCES

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Bird migration. Springer, pp 331–351

Austin RE, De Pascalis F, Arnould JP, et al (2019) A sex-influenced flexible foraging strategy in a tropical seabird, the magnificent frigatebird. Marine Ecology Progress Series 611:203–214

Barbraud C, Delord K, Kato A, et al (2021) Sexual segregation in a highly pagophilic and sexually dimorphic marine predator. Peer Community Journal 1:e71. DOI: 10.24072/pcjournal.75. bioRxiv 472431

Becker J (2014) Dispersal and Genetic Variation in a Naturally Fragmented Environment: Insights from a Long-term Study of White-throated Dippers (Cinclus cinclus). Doctoral dissertation, University of Zurich. https://www.zora.uzh.ch/id/eprint/102335/1/BeckerPhilipp_PhD-thesis_2014.pdf. Accessed on 29/07/2022

Behera SK, Yamagata T (2001) Subtropical SST dipole events in the southern Indian Ocean. Geophysical Research Letters 28:327–330

Belkin, IM, Gordon, AL (1996) Southern Ocean fronts from the Greenwich meridian to Tasmania. Journal of Geophysical Research: Oceans, 101(C2), 3675-3696

Boynton CK, Mahony NA, Williams TD (2020) Barn Swallow (Hirundo rustica) fledglings use crop habitat more frequently in relation to its availability than pasture and other habitat types. The Condor 122:duz067

Bruner JS (1972) Nature and uses of immaturity. American psychologist 27:687

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. NewYork,NY.

Burns JM, Clark CA, Richmond JP (2004) The impact of lactation strategy on physiological development of juvenile marine mammals: implications for the transition to independent foraging. Elsevier, pp 341–350

Campioni L, Dias MP, Granadeiro JP, Catry P (2020) An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. Journal of Animal Ecology 89:29–43

Campioni L, Granadeiro JP, Catry P (2016) Niche segregation between immature and adult seabirds: does progressive maturation play a role? Behavioral Ecology 27:426–433

Caubet Y, Jaisson P, Lenoir A (1992) Preimaginal induction of adult behaviour in insects. The Quarterly Journal of Experimental Psychology Section B 44:165–178

Clay TA, Joo R, Weimerskirch H, et al (2020) Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. Journal of Animal Ecology 89:1811–1823

Collet J, Prudor A, Corbeau A, et al (2020) First explorations: ontogeny of central place foraging directions in two tropical seabirds. Behavioral Ecology 31:815–825

Corbeau A, Prudor A, Kato A, Weimerskirch H (2020b) Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. Journal of Animal Ecology 89:20–28. https://doi.org/10.1111/1365-2656.13121

Daunt F, Afanasyev V, Adam A, et al (2007) From cradle to early grave: juvenile mortality in European shags Phalacrocorax aristotelis results from inadequate development of foraging proficiency. Biology Letters 3:371–374. https://doi.org/10.1098/rsbl.2007.0157

de Grissac S, Bartumeus F, Cox SL, Weimerskirch H (2017) Early-life foraging: Behavioral responses of newly fledged albatrosses to environmental conditions. Ecology and evolution 7:6766–6778

de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. Scientific reports 6:26103

Delord K, Barbraud C, Bost CA, et al (2013) Atlas of top predators from the French Southern Territories in the Southern Indian Ocean. http://www.cebc.cnrs.fr/ecomm/Fr_ecomm/ecomm_ecor_OI1.html

Delord K, Cotté C, Terray P, et al (2021) Factors affecting adult body condition in the endangered northern rockhopper penguin. Marine Biology 168:1–15

Dukas R (2006) Learning in the context of sexual behaviour in insects. Animal Biology 56:125–141

Ellis HI, Gabrielsen GW (2002) Energetics of free-ranging seabirds. In: Seabirds energetics, Whittow, G. C. and Rahn, H. Plenum Press, N.Y., pp 359–408

Evans DR (2018) The post-fledging survival and movements of juvenile Barn Swallows (Hirundo rustica): an automated telemetry approach. Electronic Thesis and Dissertation Repository. 5791. https://ir.lib.uwo.ca/etd/5791. Accessed on 29/07/2022

Fay R, Weimerskirch H, Delord K, Barbraud C (2015) Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. Journal of Animal Ecology 84:1423–1433

Frankish CK, Manica A, Clay TA, et al (2022) Ontogeny of movement patterns and habitat selection in juvenile albatrosses. Oikos e09057

Frankish CK, Manica A, Phillips RA (2020a) Effects of age on foraging behavior in two closely related albatross species. Movement ecology 8:7

Frankish CK, Phillips RA, Clay TA, et al (2020b) Environmental drivers of movement in a threatened seabird: insights from a mechanistic model and implications for conservation. Diversity and Distributions 26:1315–1329

Furness RW (1988) Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed albatross Diomedea chlororhynchos. J Zool 215:719–727

Gonzales-Solis J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels Macronectes halli during incubation. Oikos 90:390–398

Gutowsky SE, Gutowsky LF, Jonsen ID, et al (2014) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. Movement ecology 2:23–23

Harel R, Horvitz N, Nathan R (2016) Adult vultures outperform juveniles in challenging thermal soaring conditions. Scientific reports 6:27865. https://doi.org/10.1038/srep27865

Heyes CM (1994) Social learning in animals: categories and mechanisms. Biological Reviews 69:207–231

Jaeger A, Jaquemet S, Phillips RA, et al (2013) Stable isotopes document inter- and intra-specific variation in feeding ecology of nine large southern Procellariiformes. Mar Ecol Prog Ser 490:255–266

Jouventin P, Martinez J, Roux J-P (1989) Breeding biology and current status of the Amsterdam Island Albatross *Diomedea amsterdamensis*. Ibis 131(2):171-182

King JR (1974) Seasonal allocation of time and energy resources in birds. Avian energetics 4–85

Krüger S, Reid T, Amar A (2014) Differential range use between age classes of southern African Bearded Vultures Gypaetus barbatus. PLoS One 9(12), e114920. DOI: 10.1371/journal.pone.0114920

Lack D (1954) The natural regulation of animal numbers. The Natural Regulation of Animal Numbers

Langen TA (1996) Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, Calocitta formosa. Animal Behaviour 51:575–588

Langston NE, Rohwer S (1996) Molt-breeding tradeoffs in albatrosses : life history implications for big birds. Oikos 76:498–510

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. Journal of statistical software 25:1–18

Lewis S, Benvenuti S, Dall–Antonia L, et al (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proceedings of the Royal Society of London Series B: Biological Sciences 269:1687–1693

Lin X, Zhang D (1999) Inference in generalized additive mixed modelsby using smoothing splines. Journal of the royal statistical society: Series b (statistical methodology) 61:381–400

Louzao M, Wiegand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Movement ecology 2:1–15

Lovich JE, Gibbons JW (1992) A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging 56:269–269

Mackley EK, Phillips RA, Silk JR, et al (2010) Free as a bird? Activity patterns of albatrosses during the nonbreeding period. Marine Ecology Progress Series 406:291–303

Marchetti K, Price T (1989) Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biological Reviews 64:51–70

Margrath R, Lill A (1985) Age-related differences in behaviour and ecology of crimson rosellas, Platycercus elegans, during the non-breeding season. Wildlife Research 12:299–306

Martin P, Bateson P (1985) The ontogeny of locomotor play behaviour in the domestic cat. Animal behaviour 33:502–510

Mendez L, Prudor A, Weimerskirch H (2017) Ontogeny of foraging behaviour in juvenile red-footed boobies (Sula sula). Scientific reports 7:1–11

Murphy ME (1996) Energetics and nutrition of molt. In: Avian energetics and nutritional ecology. Springer, pp 158–198

Mushinsky HR, Hebrard JJ, Vodopich DS (1982) Ontogeny of water snake foraging ecology. Ecology 63:1624–1629

Naef-Daenzer B, Grüebler MU (2008) Post-fledging range use of Great Tit Parus major families in relation to chick body condition. Ardea 96:181–190

Nevitt GA, Losekoot M, Weimerskirch H (2008) Evidence for olfactory search in wandering albatross, Diomedea exulans. Proceedings of the National Academy of Sciences 105:4576–4581

Nourani E, Vansteelant WMG, Byholm P, Safi K (2020) Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. Biology Letters 16:20190797. https://doi.org/10.1098/rsbl.2019.0797

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of Ecological Systems, Ohio State University Press. Columbus, pp 154–177

Pajot A, Corbeau A, Jambon A, Weimerskirch H (2021) Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. Journal of Avian Biology 52: e02597. https://doi.org/10.1111/jav.02597

Payo-Payo A, Genovart M, Bertolero A, et al (2016) Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. Proceedings of the Royal Society B: Biological Sciences 283:20153042

Peery MZ, Henkel LA, Newman SH, et al (2008) Effects of rapid flight-feather molt on postbreeding dispersal in a pursuit-diving seabird. The Auk 125:113–123

Pennycuick CJ (1982) The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Phil Trans R Soc Lond 300:75–106

Péron C, Grémillet D (2013) Tracking through Life Stages: Adult, Immature and Juvenile Autumn Migration in a Long-Lived Seabird. Plos One 8:e72713

Phalan B, Phillips RA, Silk JR, et al (2007) Foraging behaviour of four albatross species by night and day. Marine Ecology Progress Series 340:271–286

Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Marine Ecology Progress Series 578:117–150

Phillips RA, Mcgill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Marine Biology 158:2199–2208

Phillips RA, Silk JRD, Croxall JP, et al (2004a) Accuracy of geolocation estimates for flying seabirds. Marine Ecology-Progress Series 266:265–272

Phillips RA, Silk JRD, Phalan B, et al (2004b) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proceedings of the Royal Society of LondonSeries B: Biological Sciences 271:1283–1291

Rapaport LG, Brown GR (2008) Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews 17:189–201

Ricklefs RE (1977) On the evolution of reproductive strategies in birds: reproductive effort. American naturalist 111:453–478

Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. Studies of Avian biology 8:84–94

Riotte-Lambert L, Weimerskirch H (2013) Do naive juvenile seabirds forage differently from adults? Proceedings of the Royal Society B: Biological Sciences 280:20131434

Rivalan P, Barbraud C, Inchausti P, Weimerskirch H (2010) Combined impact of longline fisheries and climate on the persistence of the Amsterdam albatross. Ibis 152:6–18

Rotics S, Kaatz M, Resheff YS, et al (2016a) The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. Journal of Animal Ecology 85:938–947

Rotics S, Turjeman S, Kaatz M, et al (2021) Early-life behaviour predicts first-year survival in a long-distance avian migrant. Proceedings of the Royal Society B 288:20202670

Roux JP, Jouventin P, Mougin JL, et al (1983) Un nouvel albatros Diomedea amsterdamensis n. sp. découvert sur l'île Amsterdam (37°50'S, 77°35'E). L'Oiseau et R F O 53:1–11

Ruaux G, Lumineau S, de Margerie E (2020) The development of flight behaviours in birds. Proceedings of the Royal Society B 287:20200668

Sergio F, Tanferna A, De Stephanis R, et al (2014) Individual improvements and selective mortality shape lifelong migratory performance. Nature 515:410–413

Shaffer SA, Weimerskirch H, Costa D (2001) Functional significance of sexual dimorphism in wandering albatrosses, Diomedea exulans. Functional Ecology 15:203–210

Smith RJ (1999) Statistics of sexual size dimorphism. Journal of Human Evolution 36:423–458. https://doi.org/10.1006/jhev.1998.0281

Stauss C, Bearhop S, Bodey T, et al (2012) Sex-specific foraging behaviour in northern gannets Morus bassanus: incidence and implications. Marine Ecology Progress Series 457:151–162

Stearns SC (1992) The Evolution of Life Histories, Oxford: Oxford University Press.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. Accessed 29/07/2022

Terray P (2011) Southern Hemisphere extra-tropical forcing: a new paradigm for El Niño-Southern Oscillation. Climate dynamics 36:2171–2199

Thiebot J-B, Delord K, Marteau C, Weimerskirch H (2014) Stage-dependent distribution of the critically endangered Amsterdam albatross in relation to Economic Exclusive Zones. Endangered Species Research 23:263–276

Thiers L, Delord K, Barbraud C, et al (2014) Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. Mar Ecol Prog Ser 499:233–248

Thorup K, Alerstam T, Hake M, Kjellén N (2003) Bird orientation: compensation for wind drift in migrating raptors is age dependent. Proceedings of the Royal Society of London Series B: Biological Sciences 270:S8–S11

Urios V, López-López P, Limiñana R, Godino A (2010) Ranging behaviour of a juvenile Bearded Vulture (Gypaetus barbatus meridionalis) in South Africa revealed by GPS satellite telemetry. Ornis Fennica, 87(3), 114

Votier SC, Grecian WJ, Patrick S, Newton J (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Marine biology 158:355–362

Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Advances in marine biology 54:107–170

Weimerskirch H (1991) Sex-specific differences in molt strategy in relation to breeding in the wandering albatross. Condor 93:731–737

Weimerskirch H, Akesson S, Pinaud D (2006) Postnatal dispersal of wandering albatrosses *Diomedea exulans*: implications for the conservation of the species. J Avian Biol 37:23–28

Weimerskirch H, Brothers N, Jouventin P (1997a) Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationship with long-line fisheries: conservation implications. Biological conservation 79:257–270

Weimerskirch H, Cherel Y, Delord K, et al (2014) Lifetime foraging patterns of the wandering albatross: Life on the move! Journal of Experimental Marine Biology and Ecology 450:68–78

Weimerskirch H, de Grissac S, Ravache A, et al (2020) At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. Marine Ecology Progress Series 633:225–238

Weimerskirch H, Delord K, Guitteaud A, et al (2015a) Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Scientific Reports 5:8853-

Weimerskirch H, Guionnet T (2002) Comparative activity pattern during foraging of four albatross species. Ibis 144:40–50

Weimerskirch H, Shaffer SA, Tremblay Y, et al (2009) Species-and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Marine Ecology Progress Series 391:267–278

Weimerskirch H, Tarroux A, Chastel O, et al (2015b) Population-specific wintering distributions of adult south polar skuas over the three oceans. Mar Ecol Prog Ser 538:229–237

Weimerskirch H, Wilson RP, Lys P (1997b) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Marine Ecology Progress Series 151:245–254

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. American naturalist 687–690

Wilson RP, Ducamp JJ, Rees G, et al (1992) Estimation of location: global coverage using light intensity. In: Priede IMSS (ed). Ellis Horward, Chichester, pp 131–134

Wood S (2015) Package 'mgcv.' R package version 1:729

Wood S (2017) Generalized Additive Models: An Introduction with R, 2nd Edition Chapman and Hall//CRC, Boca Raton. Chapman and Hall/CRC

Wynn J, Padget O, Mouritsen H, et al (2020) Natal imprinting to the Earth's magnetic field in a pelagic seabird. Current Biology 30:2869–2873

Ydenberg RC (1989) Growth-mortality trade-offs and the evolution of juvenile life histories in the alcidae. Ecology 70:1494–1506

Ydenberg RC, Welham CVJ, Schmid-Hempel R, et al (1992) Time and energy constraints and the relationships between currencies in foraging theory. Behavioral Ecology 5:28–34

Yoda K, Kohno H, Naito Y (2004) Development of flight performance in the brown booby. Proceedings of the Royal Society of London Series B: Biological Sciences 271:S240–S242

Zuur AF (2009a) Mixed effects models and extensions in ecology with R, NY: Springer. Springer, New York

Zuur AF (ed) (2009b) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Supplementary

Species biological aspects

Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021). Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997). However, this strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a more important utilization of the '*sit-and-wait*' technique and possibly to vary depending on sites suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter bouts on the water in the former technique (compared to '*foraging-in-flight*').

Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale migratory movements reaching >4000 km from the colony exploiting continuously warm waters (~18°C). No clear longitudinal seasonality existed in the movements of adults, nonetheless they tended to move westwards in June/July and eastwards in November. The immature birds moved widely in longitude (0° to 135° E), exploiting exclusively warm waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity existed in the movements, except that they also tended to move westwards in June and eastwards in November. Juveniles exhibited very large post-fledging movement capacities over the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal gradient (27° to 47° S). Juveniles birds tended to move westwards first in March-April and temporarily exhibited synchronous individual movements. De Grissac et al. (2016) compared trajectories (i.e. departure direction or orientation toward specific areas) of juveniles and adults and showed that juveniles performed an initial rapid movement taking all individuals away from the vicinity of their native colony, and in a second time performed large-scale movements similar to those of adults during the sabbatical period. High individual variability and no clear differences between juveniles and adults patterns were found, except that adults foraged at significantly higher latitudes. De Grissac et al. (2016) concluded in an overlap in distribution between adults and juveniles due to the extensive area they used and their differences in latitudinal distribution compared to other Procellariiformes species.

Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch 1991). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting important constraints that could compete with breeding (immature birds tend to renew fewer feathers compared to adult breeders), and particularly in females (Weimerskirch 1991). In smaller sized seabirds, a link between moulting pattern and activity parameters was evidenced, resulting in a clear temporal pattern partly explained by moult (Cherel et al. 2016). Recently Gutowsky et al. (2014) suggested that tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could compromise flight from active wing moult during the nonbreeding period and induce changes in daily activity budget during a ‘quasi-flightless’ stage. However, there is no such data for southern albatrosses. Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested it such a compromise. However, adult birds during the non-breeding season appear to spend much more time on the water during winter, suggesting that partial moult may occur at this time, as observed in many other seabird species that have to moult during the non-breeding season and show reduced activity during specific periods that may correspond to moulting (Weimerskirch et al. 2015, 2020).

Table S1 Hypotheses and predictions about the factors driving differences in activity (time spent on water, number and duration of flying bouts, number and duration of water bouts) year-round in Amsterdam albatrosses

	Predictions		
Hypothesis	Time spent on water (%)	Flying bouts (number/duration)	Water bouts (number/duration)
~~(A) Sex-specific body size~~	~~Behavioural difference maintained throughout the cycle: lower time spent on water for females compared to males~~ ~~Alternative prediction: no specific prediction due to trade-off between duration and number of bouts~~	~~Behavioural difference maintained throughout the cycle: females sustain shorter flying bouts but more numerous compared to males~~	~~Behavioural difference maintained throughout the cycle: females sustain longer water bouts duration but less numerous compared to males~~
(A~~B~~) Age and stage specific	Juveniles: increased foraging time/effort and thus lower time spent on water than other stages	Juveniles: increased foraging time/effort and thus longer flying bouts than other stages	Juveniles: increased foraging time/effort and thus shorter water bouts than other stages
(B~~C~~) Temporal change	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: ~~improvement of~~change in foraging skills (lower time spent on water) corresponding to gradual change with less time sitting on water during the 1st month after fledging	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: ~~improvement of~~change in foraging skills corresponding to gradual change with increasing flying bouts duration and number during the 1st months after fledging	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: ~~improvement of~~change in foraging skills corresponding to gradual change with decreasing water bouts duration and number during the 1st months after fledging

	Following departure from the colony adjustment in foraging effort or moult constraints	Adjustment in foraging effort or moult constraints according to time elapsed since departure	Adjustment in foraging effort or moult constraints according to time elapsed since departure
(C~~D~~) Seasonal environmental change	Progressive adjustment during the months of the year in foraging effort to energetic requirements or moult constraints.	Progressive adjustment during the months of the year in foraging effort to energetic requirements or moult constraints.	Progressive adjustment during the months of the year in foraging effort to energetic requirements or moult constraints.
	Higher time spent on water during moulting	Lower flying bouts duration and number during moulting	Higher water bouts duration and number during moulting
(D) Sex-specific body size	Behavioural difference maintained throughout the cycle: lower time spent on water for females compared to males Alternative prediction: no specific prediction due to trade-off between duration and number of bouts	Behavioural difference maintained throughout the cycle: females sustain shorter flying bouts but more numerous compared to males	Behavioural difference maintained throughout the cycle: females sustain longer water bouts duration but less numerous compared to males

Table S2 Selected models testing for the effects of sex, stage, number of months spent since departure (monthelap: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on) on activity parameters of Amsterdam albatrosses

	Model #	Study variable[1]	Model structure	Sample size
All stages	gamm1	PC1S	~s(monthelap, k = 2) + monthf + stade + sex + s(monthelap, device_code[2], bs = "re")~~~s(monthelap,k=2,bs="cs")+month+stage+sex,random = ~(1+ monthelap|device_code)~~	8094
All stages	gamm2	PC2S	~ s(monthelap, k = 3) + monthf + stade + s(monthelap, device_code, bs = "re")~~~s(monthelap,k=3,bs="cs")+month+stage+sex,random = ~(1+ monthelap|device_code)~~	8094
All stages	gamm3	PC3S	~monthf+stade+sex+s(monthelap,device_code, bs='re')~~~s(monthelap,k=2,bs="cs")+ month+stage+sex,random = ~(1+ monthelap|device_code)~~	8094
Juveniles	gamm4	PC1J	~~~~~ s(monthelap,k=2)+monthf+s(monthelap,device_code, bs='re')~~s(monthelap,k=2,bs="cs")+month,random = ~(1+ monthelap|device_code)~~	6161
Juveniles	gamm5	PC2J	~ s(monthelap, k = 2)+monthf+sex+s(monthelap, device_code, bs = "re")~~~s(monthelap,k=2,bs="cs")+month+sex,random = ~(1+ monthelap|device_code)~~	6161
Juveniles	gamm6	PC3J	~monthf+sex+s(monthelap,device_code, bs='re')~~~month+sex,random = ~(1+ monthelap|device_code)~~	6161

[1] First, second and third principal component issued from principal components analyses considering i) all stages combined (PCS) and ii) only juveniles (PCJ); [2] Individuals ~~PROPWATER: proportion of time spent on water, WETBOUTS: bouts spent on water duration and number, DRYBOUTS: bouts spent dry -flying duration and numbe~~

Mis en forme : Police :Non Gras

Mis en forme : Police :Non Gras

Table S3a ~~GLMM~~ GAMM results for the first principal components ~~proportion of time spent sitting on water~~ (~~PROPWATER~~PC1S; ~~GLMM1~~ gamm1 see Table S2~~1~~) of Amsterdam albatross modelled as a function of months spent since departure from the colony (month~~.~~elap~~f~~), ~~and~~ month of the year ~~(monthf)~~, stage and sex. Reference values are ~~1st month spent at sea (month.elapf0) and~~ January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.996	149.23	0.000
s(monthelap,device_code)	26.083	14.53	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.48	0.10	4.98	0.000
February	-0.21	0.08	-2.52	0.012
March	-0.60	0.09	-6.94	0.000
April	-0.96	0.09	-10.46	0.000
May	-0.77	0.09	-8.31	0.000
June	-0.77	0.09	-8.16	0.000
July	-0.42	0.09	-4.49	0.000
August	-0.11	0.09	-1.18	0.240
September	0.01	0.09	0.10	0.918
October	0.01	0.09	0.17	0.868
November	-0.01	0.09	-0.09	0.929
December	-0.08	0.09	-0.90	0.367
Immatures	-0.50	0.09	-5.76	0.000
Juveniles	-0.63	0.07	-9.69	0.000
Males	0.33	0.05	6.22	0.000

Table S3b ~~GLMM~~ GAMM results for the second principal components ~~proportion of time spent sitting on water~~ (~~PROPWATER~~PC2S; ~~GLMM1~~ gamm2 see Table S2~~1~~) of Amsterdam albatross modelled as a function of months spent since departure from the colony (month~~.~~elap~~f~~), ~~and~~ month of the year ~~(monthf)~~, stage and sex. Reference values are ~~1st month spent at sea (month.elapf0) and~~ January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.001	0.504	0.478
s(monthelap,device_code)	27.107	39.991	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.15	0.10	-1.53	0.126
February	0.13	0.08	1.71	0.088
March	0.16	0.08	2.00	0.046
April	0.42	0.08	5.03	0.000
May	0.40	0.08	4.99	0.000
June	0.25	0.08	3.16	0.002
July	0.23	0.08	2.92	0.004
August	0.26	0.08	3.40	0.001
September	0.48	0.08	6.22	0.000
October	0.35	0.08	4.57	0.000
November	0.34	0.08	4.41	0.000
December	0.19	0.08	2.49	0.013
Immatures	-0.12	0.08	-1.57	0.116
Juveniles	-0.18	0.06	-2.96	0.003

Table S3c ~~GLMM~~ GAMM results for the third principal components ~~proportion of time spent sitting on water~~ (~~PROPWATER~~PC3S; ~~GLMM1~~ gamm3 see Table S2~~1~~) of Amsterdam albatross modelled as a function of months spent since departure from the colony (month~~.~~elap~~f~~), ~~and~~ month of the year ~~(monthf)~~, stage and sex. Reference values are ~~1st month spent at sea (month.elapf0) and~~ January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap,device_code)	26.52	16.58	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.34	0.06	5.37	0.000
February	-0.22	0.06	-3.43	0.000
March	-0.07	0.06	-1.08	0.279
April	-0.10	0.07	-1.53	0.127
May	0.00	0.06	0.05	0.958
June	0.05	0.06	0.87	0.385
July	0.02	0.06	0.39	0.694
August	-0.04	0.06	-0.70	0.483
September	-0.06	0.06	-0.93	0.355
October	-0.10	0.06	-1.58	0.012
November	-0.16	0.06	-2.57	0.010
December	-0.23	0.06	-3.70	0.000
Immatures	-0.27	0.06	-4.61	0.000
Juveniles	-0.45	0.05	-9.12	0.000
Males	-0.14	0.04	-3,39	0.000

Table S4a ~~GLMM~~ GAMM results for the first principal components ~~proportion of time spent sitting on water~~ (~~PROPWATER~~PC1J; ~~GLMM1~~ gamm4 see Table S2~~1~~) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (month~~.~~elap~~f~~) and month of the year. Reference value is ~~1st month spent at sea (month.elapf0) and~~ January.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.922	24.12	0.000
s(monthelap,device_code)	6.506	12.20	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.10	0.09	-1.16	0.247
February	0.20	0.09	2.30	0.021
March	-0.13	0.09	-1.51	0.132
April	-0.27	0.09	-3.12	0.002
May	-0.16	0.09	-1.91	0.056
June	0.06	0.09	0.71	0.475
July	0.59	0.09	6.66	0.000
August	0.68	0.09	7.66	0.000
September	0.47	0.09	5.26	0.000
October	0.22	0.09	2.47	0.013
November	-0.05	0.09	-0.50	0.616
December	-0.04	0.09	-0.45	0.653

Table S4b GAMM results for the second principal components ~~proportion of time spent sitting on water~~ (~~PROPWATER~~PC2J; ~~GLMM1~~ gamm5 see Table S2~~1~~) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (month~~.~~elap~~f~~) and month of the year. Reference value is ~~1st month spent at sea (month.elapf0) and~~ January.

Variable	Smoother edf	F-test	p-value
s(monthelap)	1.000	2.40	0.122
s(monthelap,device_code)	6.813	55.91	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.05	0.12	-0.43	0.668
February	-0.27	0.08	-3.54	0.000
March	-0.14	0.08	-1.88	0.061
April	0.12	0.07	1.61	0.107
May	0.08	0.08	1.02	0.306
June	0.01	0.08	0.14	0.886
July	0.08	0.08	1.05	0.293
August	0.12	0.08	1.47	0.141
September	0.30	0.08	3.84	0.000
October	0.18	0.08	2.33	0.020
November	0.19	0.08	2.44	0.015
December	0.20	0.08	2.49	0.013
Male	-0.17	0.06	-2.78	0.005

Table S4c ~~GLMM~~ GAMM results for the third principal components ~~proportion of time spent sitting on water~~ (~~PROPWATER~~PC3J; ~~GLMM1~~ gamm5 see Table S2~~1~~) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (month~~.~~elap~~f~~), month of the year and sex. Reference value are ~~1st month spent at sea (month.elapf0) and~~ January and females.

Variable	Smoother edf	F-test	p-value
s(monthelap,device_code)	7.724	19.37	0.000

	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.04	0.05	-0.77	0.444
February	-0.10	0.06	-1.59	0.113
March	-0.13	0.06	-2.19	0.029
April	-0.06	0.06	-0.94	0.349
May	0.02	0.06	0.37	0.715
June	0.13	0.06	2.11	0.035
July	0.02	0.06	0.25	0.802
August	0.00	0.06	0.01	0.992
September	0.00	0.06	0.01	0.996
October	-0.04	0.06	-0.59	0.556
November	-0.06	0.07	-0.85	0.395
December	0.02	0.06	0.34	0.735
Male	0.10	0.05	1.89	0.059

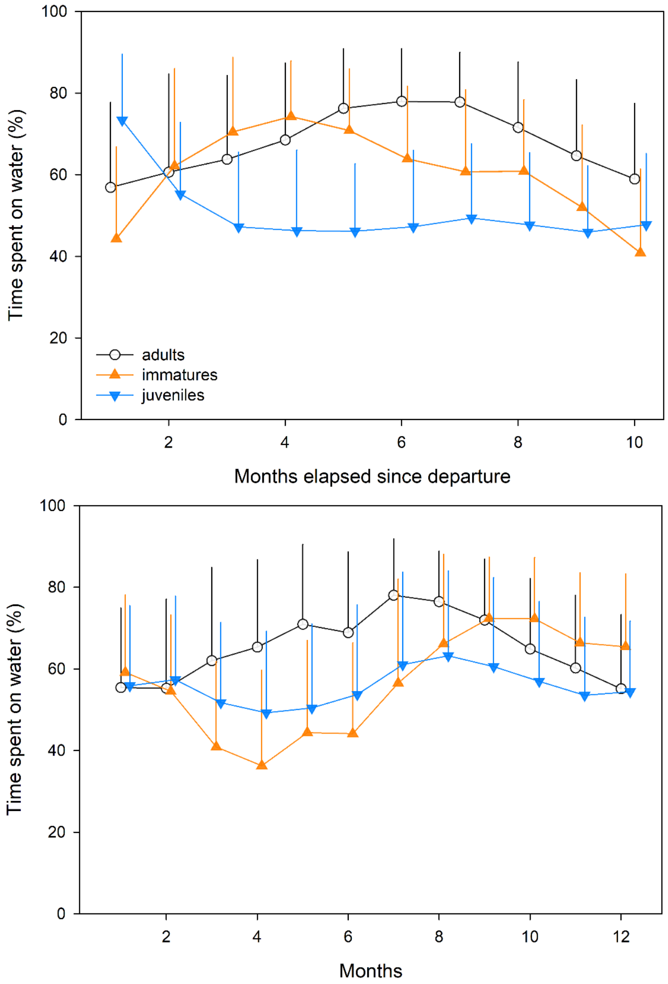
FIGURES

~~Figure S7 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd.~~

~~Figure S8 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd.~~

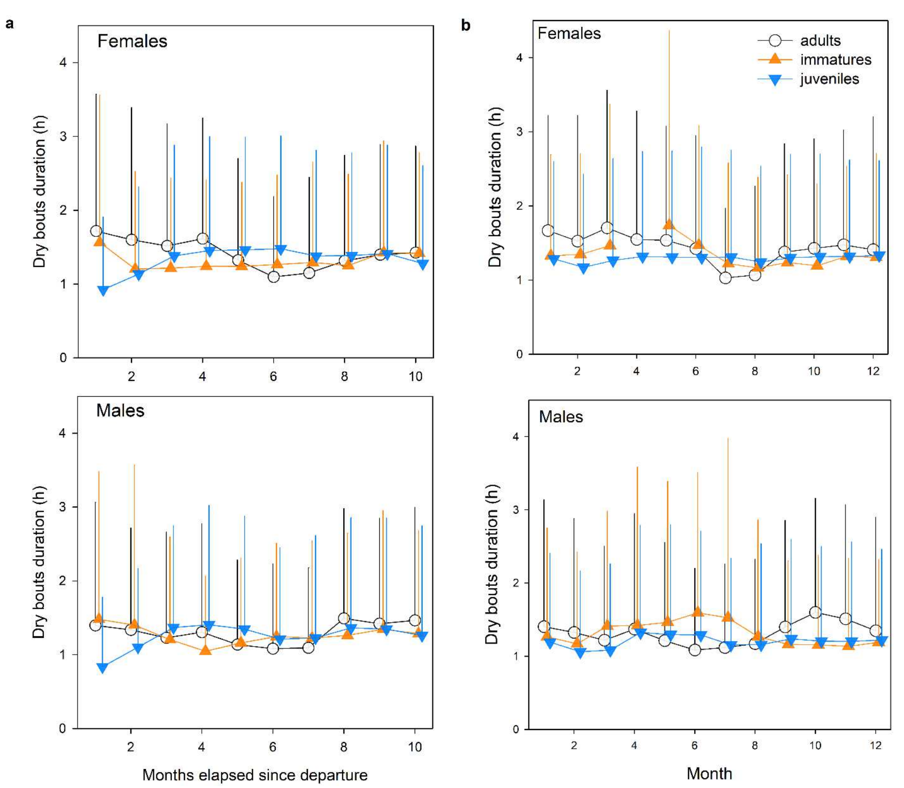
~~Figure S9 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd.~~

~~Figure S10 Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd.~~



S

Figure S1 Daily proportions of time spent on water depending on stage (juveniles, immatures and adults) for every month since departure from the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd



2803

2804 Figure S2 Daily flying bouts duration (dry bouts in hours) depending and on sex (females and males) and
2805 on stage (juveniles, immatures and adults) for a) time elapsed since departure from the colony expressed
2806 in month (left panel) and for b) each month of the year (right panel). One side error bars represent ± 1 sd

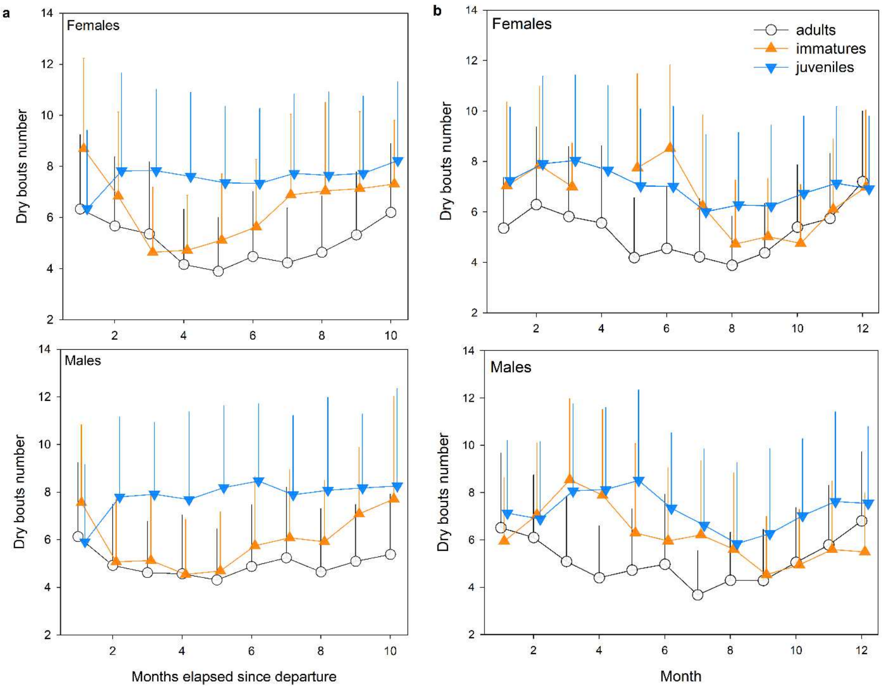


Figure S3 Daily flying bouts number (dry bouts) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

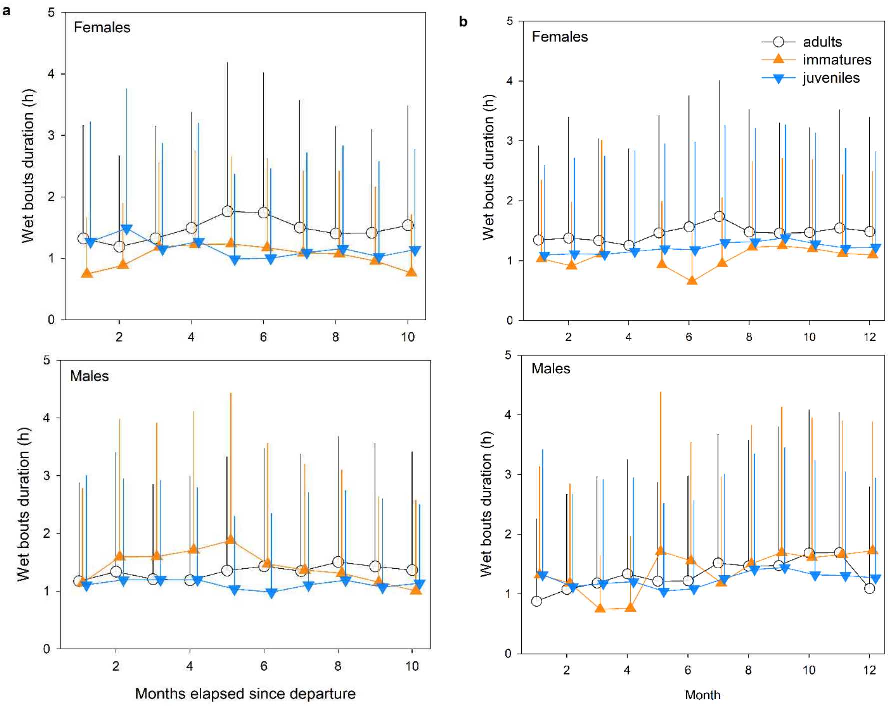


Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures and adults) and on sex (females and males) for every month since departure of the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

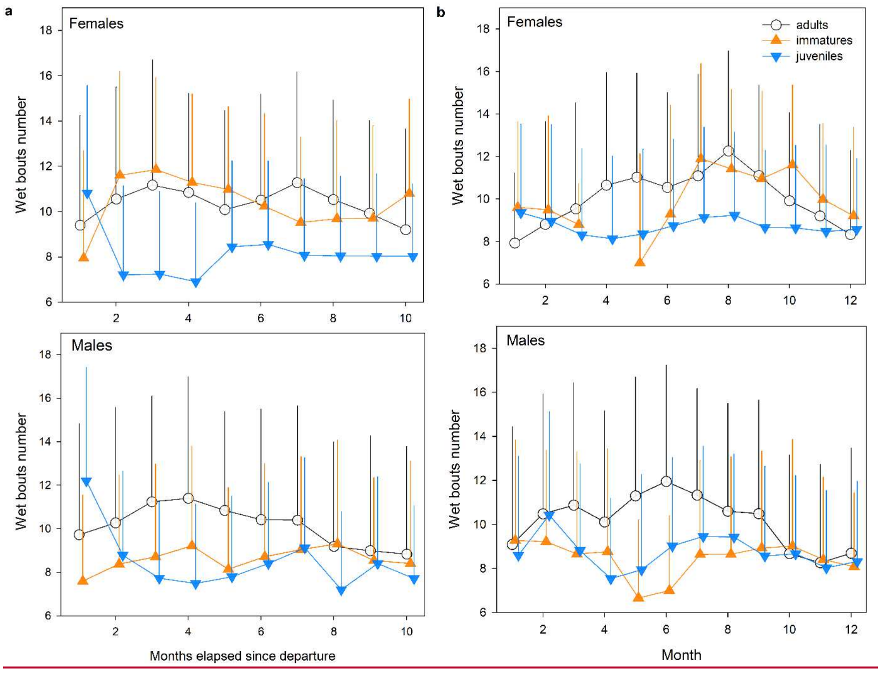


Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

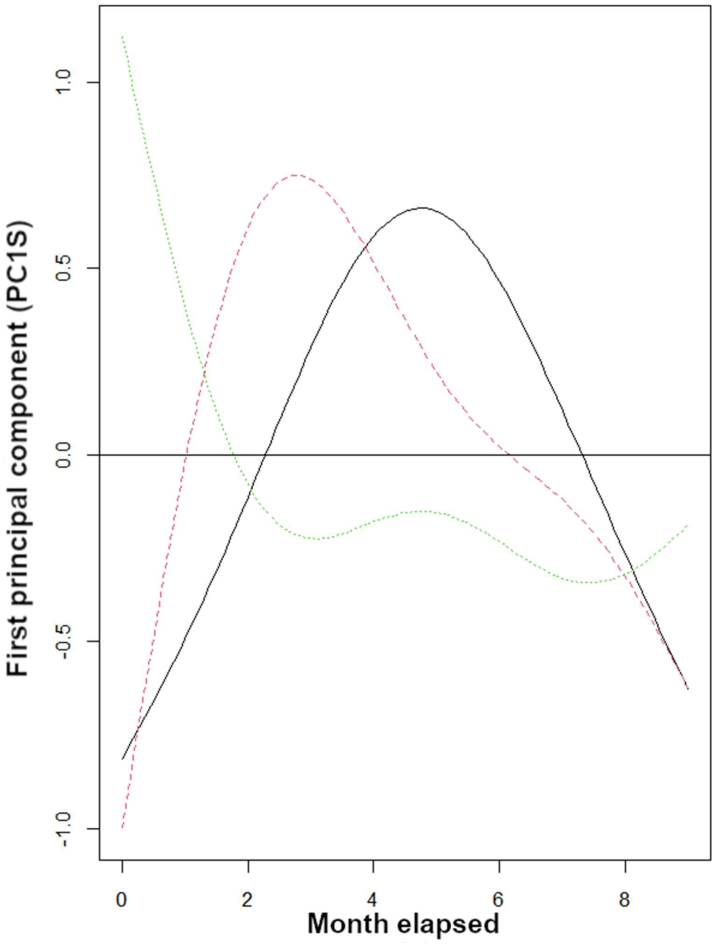
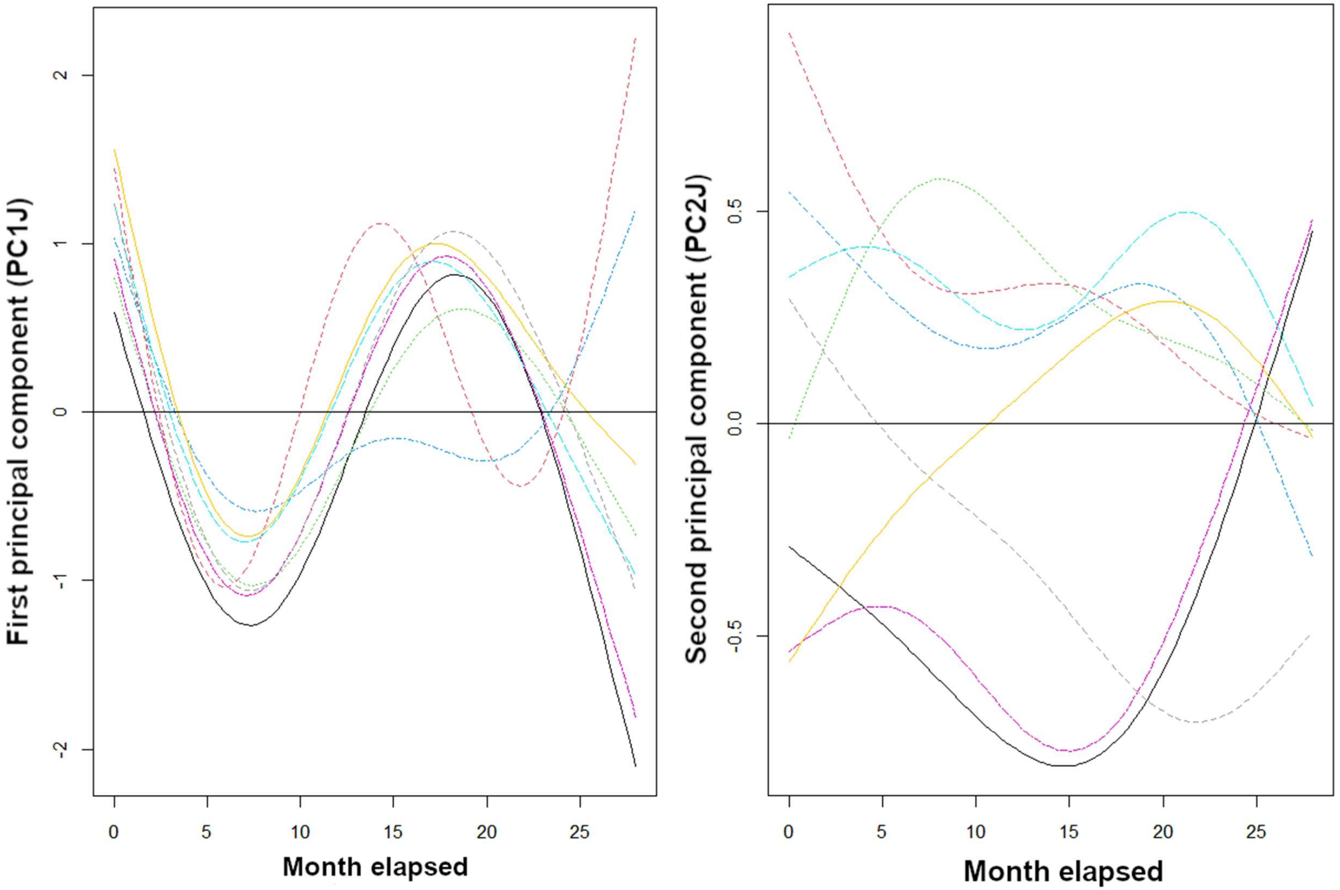
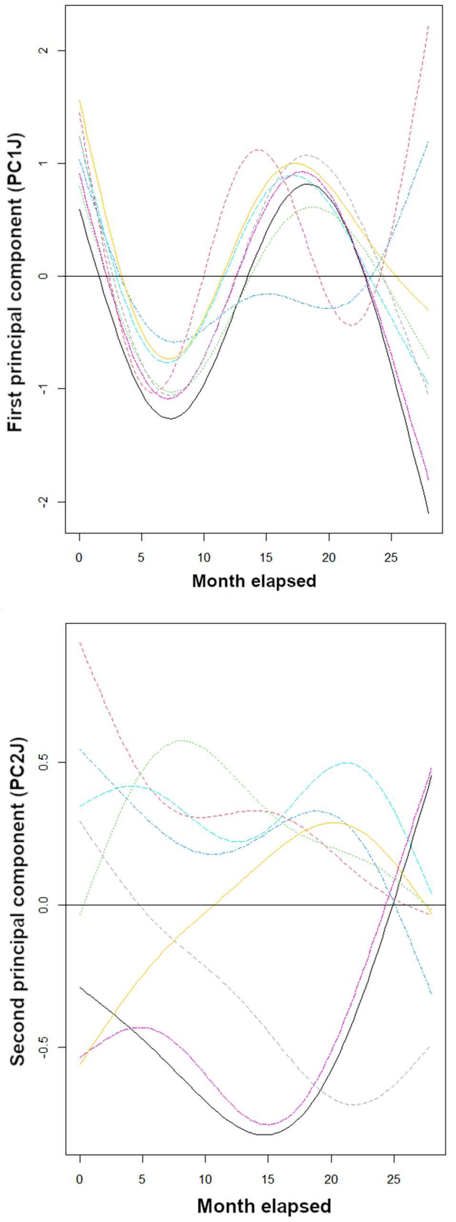


Figure S6 Modeled first axis of principal components analysis of activity parameters of all stages (i.e. adult (plain black line), immature (dashed red line) and juvenile (dotted green line)) of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model



Mis en forme : Largeur : 27,94 cm, Hauteur : 21,59 cm

Figure S7 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs obtained using random intercepts and slopes (each coloured line representing an individual). Line corresponds to estimated smoother from the GAMM models



~~7 Modeled first axis of principal components analysis of activity parameters of all stages (i.e. adult (plain black line), immature (dashed red line) and juvenile (dotted green line)) of Amsterdam~~

~~albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model.~~

~~Figure S1~~

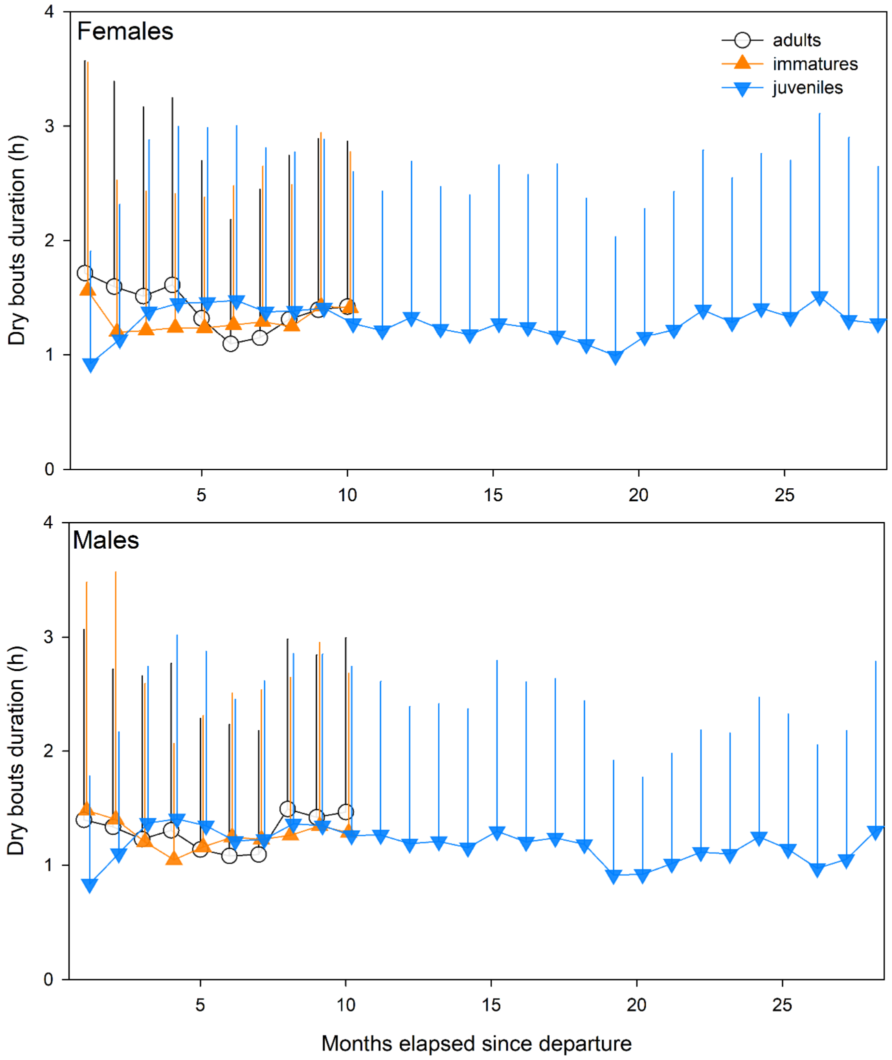
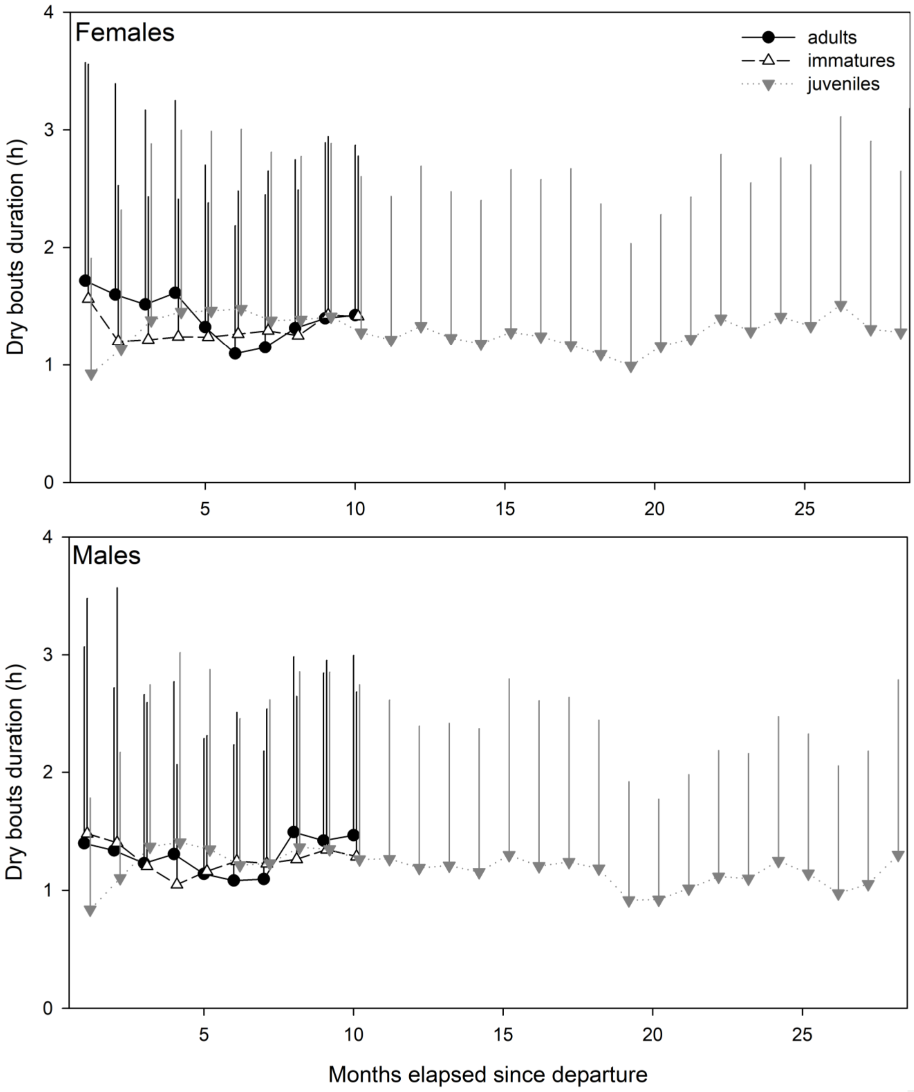


Figure S8~~7~~ Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd


Females
adults
immatures
juveniles
Dry bouts duration (h)
0
1
2
3
4
5
10
15
20
25
Males
Dry bouts duration (h)
0
1
2
3
4
5
10
15
20
25
Months elapsed since departure

~~Figure S2~~

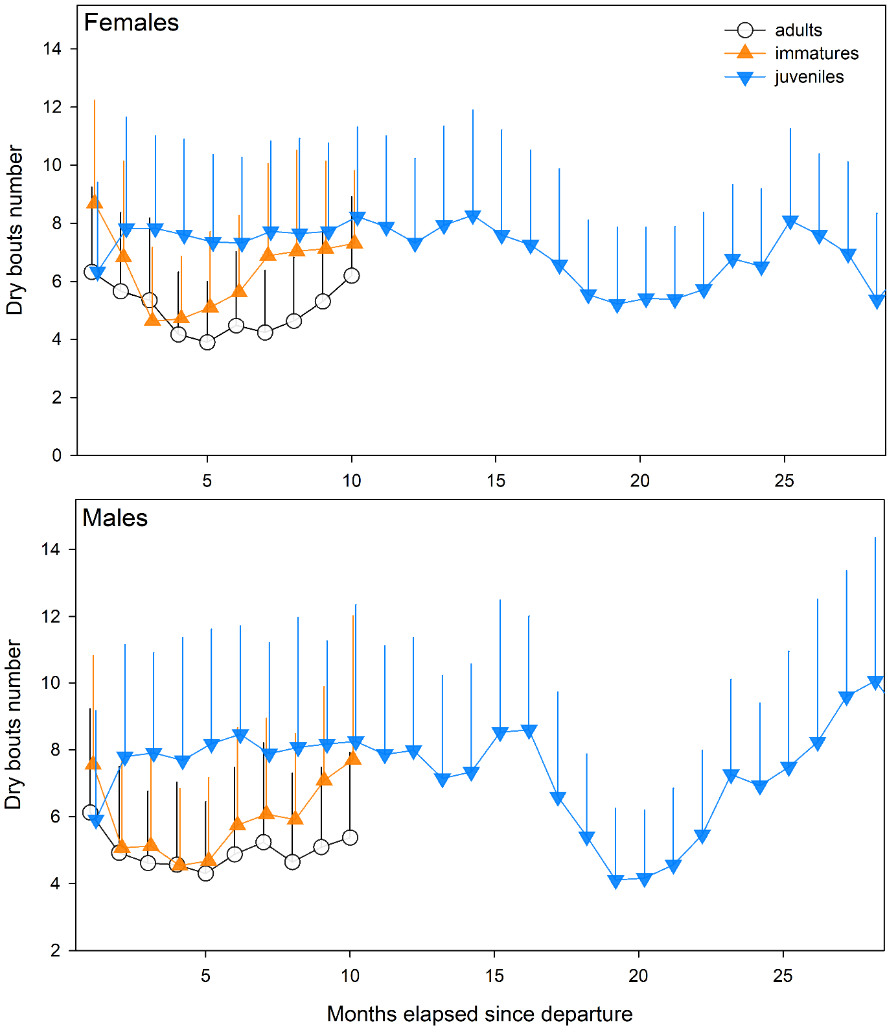
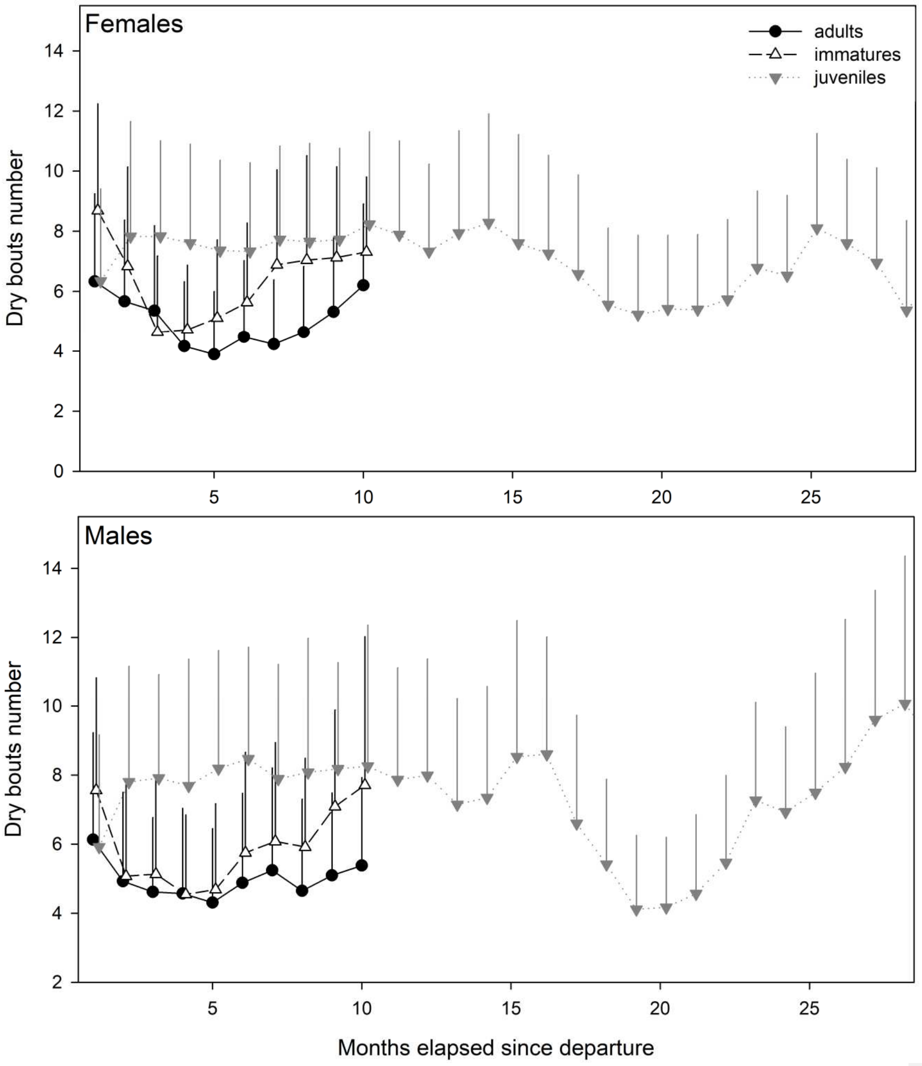
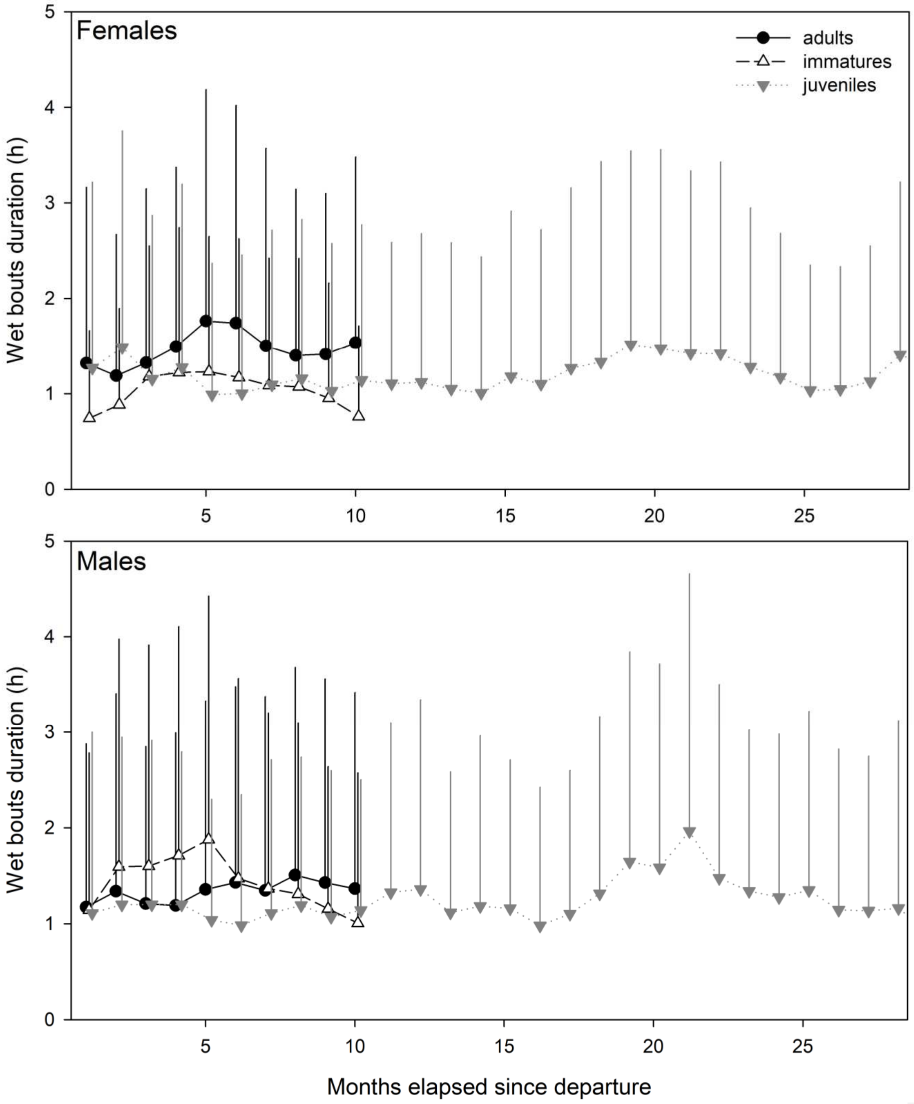


Figure S9~~8~~ Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd


Females
adults
immatures
juveniles
Dry bouts number
0
2
4
6
8
10
12
14
5
10
15
20
25
Males
Dry bouts number
2
4
6
8
10
12
14
5
10
15
20
25
Months elapsed since departure

~~Figure S3~~


Females
adults
immatures
juveniles
Wet bouts duration (h)
0
1
2
3
4
5
5
10
15
20
25
Males
Wet bouts duration (h)
0
1
2
3
4
5
5
10
15
20
25
Months elapsed since departure

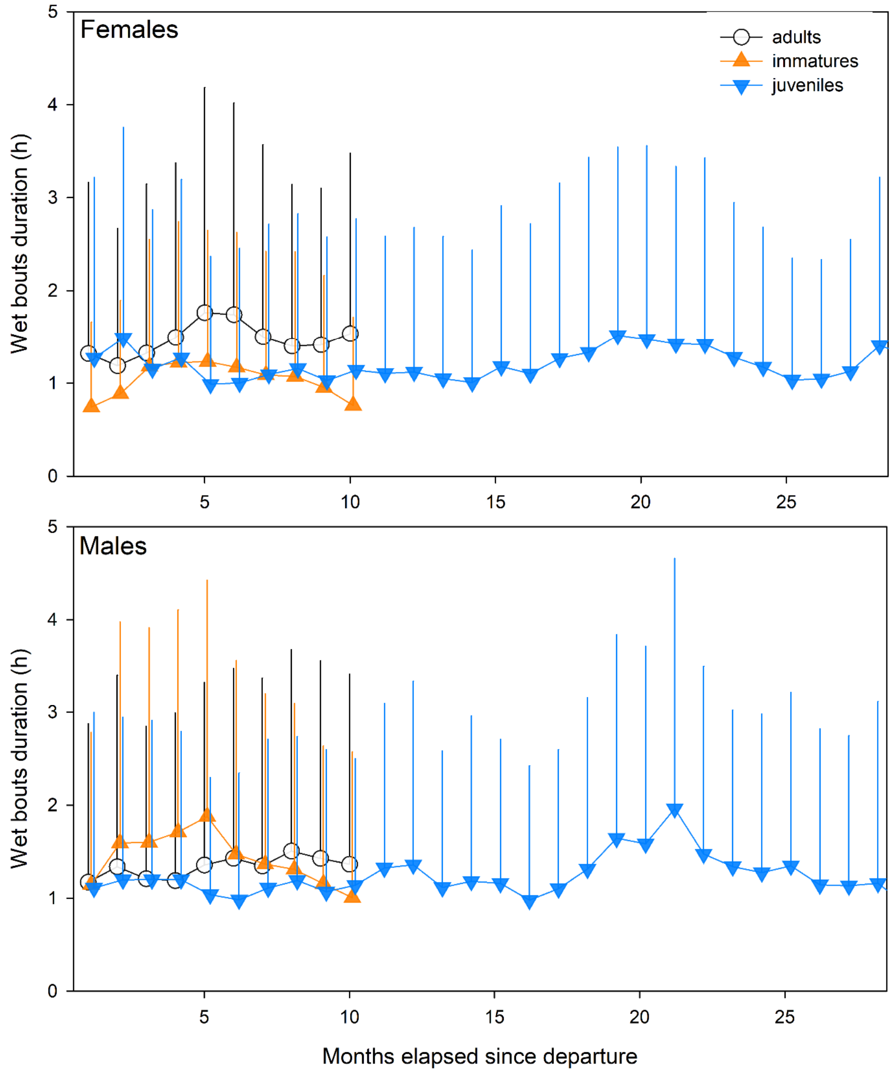


Figure S10~~9~~ Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

~~Figure S4~~

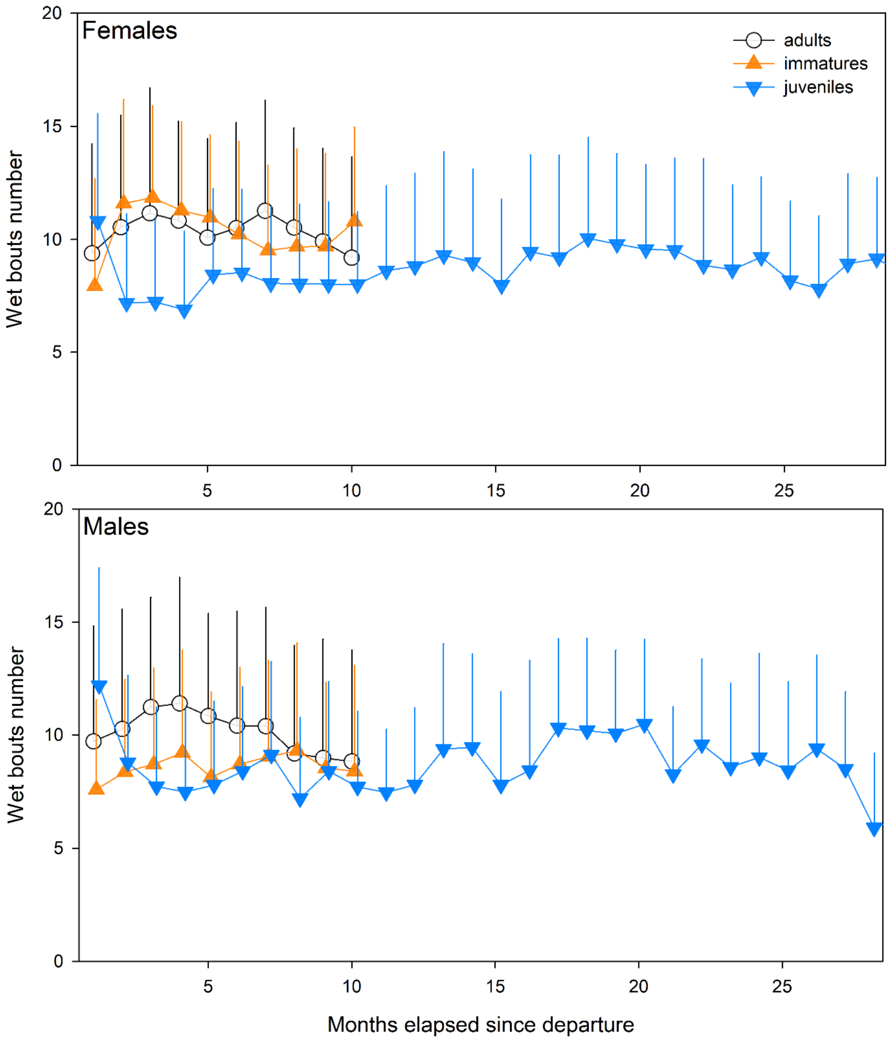


Figure S11~~0~~ Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

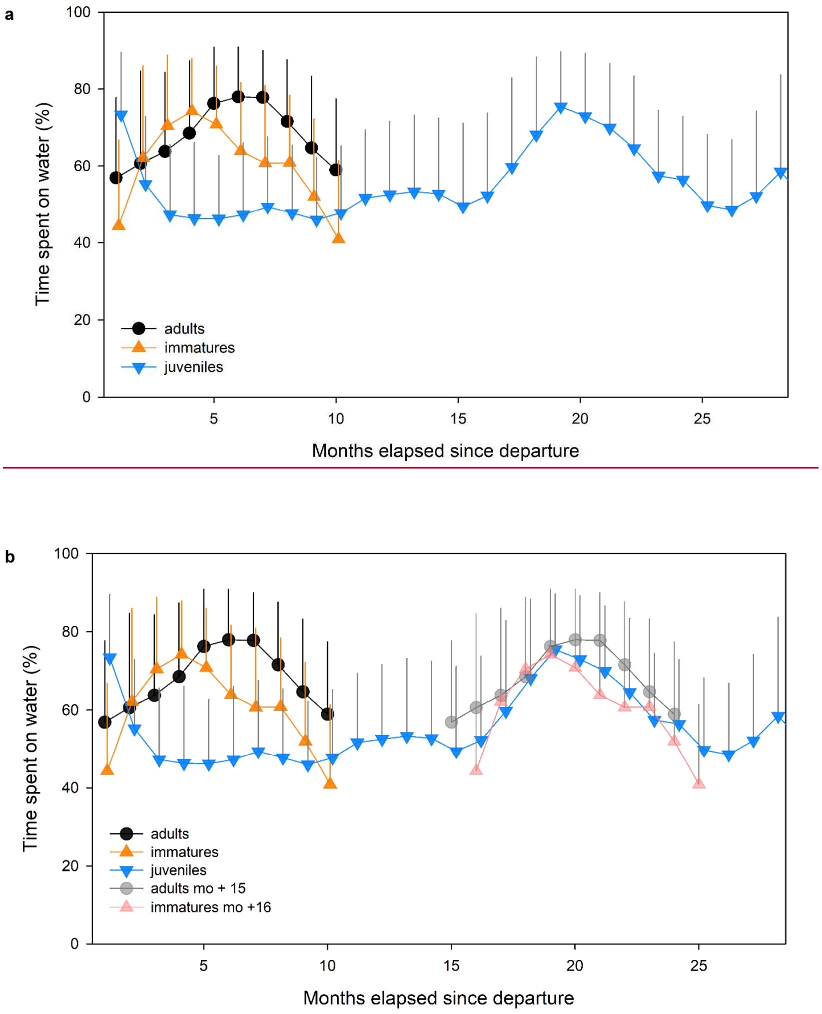
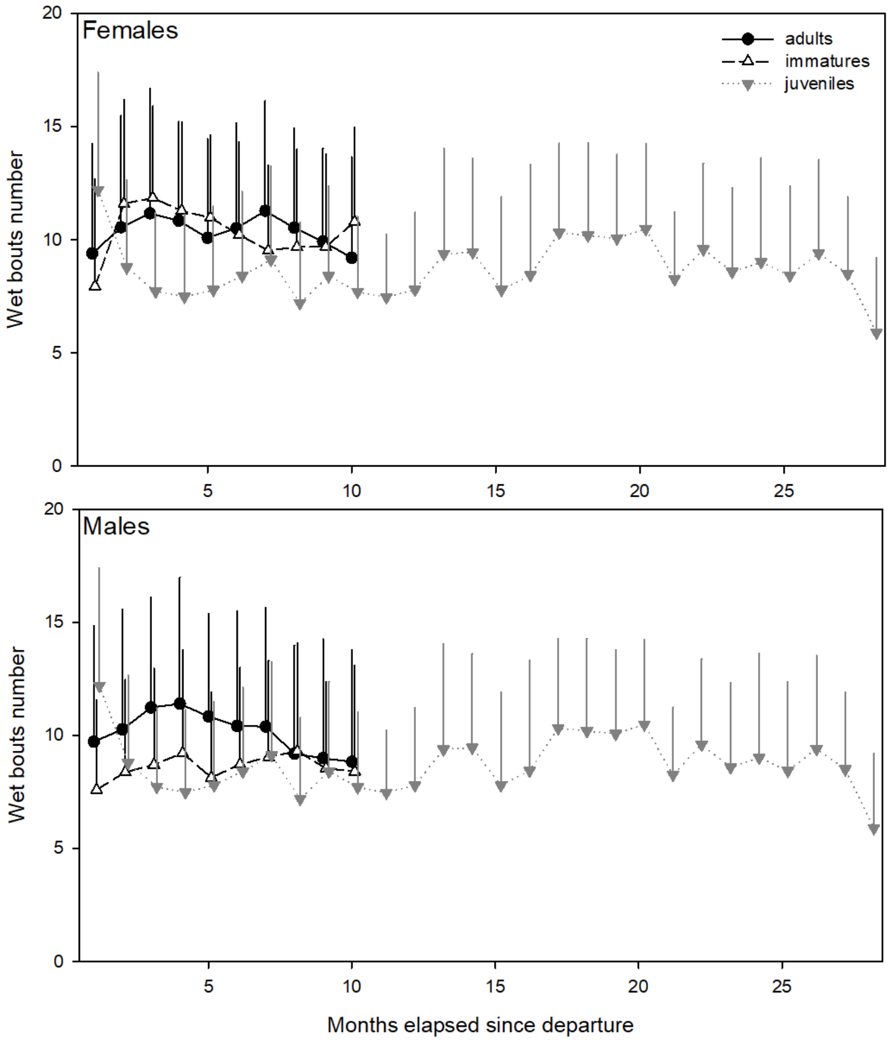


Figure S12~~1~~ Daily proportions of time spent on water for every month since departure of the colony for juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel) and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error bars represent ± 1 sd


Females
adults
immatures
juveniles
Males
Wet bouts number
Wet bouts number
0
5
10
15
20
5
10
15
20
25
Months elapsed since departure

REFERENCES

Cherel Y, Quillfeldt P, Delord K, Weimerskirch H (2016) Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. Front Ecol Environ 4:1–16

de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. Sci Rep 6:26103

Delord K, Barbraud C, Bost CA, et al (2013) Atlas of top predators from the French Southern Territories in the Southern Indian Ocean. http://www.cebc.cnrs.fr/ecomm/Fr_ecomm/ecomm_ecor_OI1.html

Ellis HI, Gabrielsen GW (2002) Energetics of free-ranging seabirds. In: Seabirds energetics, Whittow, G. C. and Rahn, H. Plenum Press, N.Y., pp 359–408

Furness RW (1988) Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed albatross Diomedea chlororhynchos. J Zool 215:719–727

Gutowsky SE, Gutowsky LF, Jonsen ID, et al (2014) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. Mov Ecol 2:23–23

Langston NE, Rohwer S (1996) Molt-breeding tradeoffs in albatrosses : life history implications for big birds. Oikos 76:498–510

Louzao M, Wiegand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Mov Ecol 2:1–15

Murphy ME (1996) Energetics and nutrition of molt. In: Avian energetics and nutritional ecology. Springer, pp 158–198

Nevitt GA, Losekoot M, Weimerskirch H (2008) Evidence for olfactory search in wandering albatross, Diomedea exulans. Proc Natl Acad Sci 105:4576–4581

Pajot A, Corbeau A, Jambon A, Weimerskirch H (2021) Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. J Avian Biol 52:

Peery MZ, Henkel LA, Newman SH, et al (2008) Effects of rapid flight-feather molt on postbreeding dispersal in a pursuit-diving seabird. The Auk 125:113–123

Phalan B, Phillips RA, Silk JR, et al (2007) Foraging behaviour of four albatross species by night and day. Mar Ecol Prog Ser 340:271–286

Thiebot J-B, Delord K, Marteau C, Weimerskirch H (2014) Stage-dependent distribution of the critically endangered Amsterdam albatross in relation to Economic Exclusive Zones. Endanger Species Res 23:263–276

Weimerskirch H (1991) Sex-specific differences in molt strategy in relation to breeding in the wandering albatross. Condor 93:731–737

Weimerskirch H, de Grissac S, Ravache A, et al (2020) At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. Mar Ecol Prog Ser 633:225–238

Weimerskirch H, Tarroux A, Chastel O, et al (2015) Population-specific wintering distributions of adult south polar skuas over the three oceans. Mar Ecol Prog Ser 538:229–237

Weimerskirch H, Wilson RP, Lys P (1997) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Mar Ecol Prog Ser 151:245–254