

1

2 PCI PCIecology

3 Decision concerning your submission

4

5 Dear Karine Delord,

6

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

10

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

13

14 When revising your article, we remind you that:

15

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

19

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

24

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

26

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

31

32 5) This disclosure has to be completed by a sentence indicating, if appropriate, that some of the authors
33 are PCI recommenders: "XY is one of the PCIecology recommenders."

34

35 **When your revised article is ready, please:**

36

37 **1) Upload the new version of your manuscript onto your favorite open archive and wait until it appears**
38 **online;**

39

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41 **PCIEcology website and go to 'For Contributors -> Your submitted preprints' in the top menu and click**
42 **on the blue 'VIEW/EDIT' button at the right end of the line referring to the preprint in question.**

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44 **3) Click on the black 'EDIT YOUR ARTICLE DATA' button (mandatory step). You can then edit the title,**
45 **authors, DOI, abstract, keywords, or disciplines. Do not forget to save your modifications by clicking on**
46 **the green button.**

47

48 **4) Click on the blue 'EDIT YOUR REPLY TO THE RECOMMENDER' button (mandatory step). You could**
49 **then write or paste your text, upload your reply as a PDF file, and upload a document with the**
50 **modifications marked in TrackChange mode. If you are submitting the final formatted version ready to**
51 **be recommended, you should only add a sentence indicating that you posted the final version on the**
52 **preprint server. Do not forget to save your modifications by clicking on the green button.**

53

54 **5) Click on the green 'SEND RESUBMISSION' button. This will result in your submission being sent to the**
55 **recommender.**

56

57 Once the recommender has read the revised version, he/she may decide to recommend it directly, in
58 which case the editorial correspondence (reviews, recommender's decisions, authors' replies) and a
59 recommendation text will be published by PCIEcology under the license CC-BY-ND.

60

61 Alternatively, other rounds of reviews may be needed before the recommender reaches a favorable
62 conclusion. He/she may also reject your article, in which case the reviews and decision will be sent to you,
63 but they will not be published or publicly released by PCIEcology. They will be safely stored in our
64 database, to which only the Managing Board has access. You will be notified by e-mail at each stage in the
65 procedure.

66

67 We thank you in advance for submitting your revised version.

68

69 Yours sincerely,

70

71 The Managing Board of PCIEcology

72 article picture

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

74 KARINE DELORD, HENRI WEIMERSKIRCH, CHRISTOPHE BARBRAUD

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

76 Submitted by Karine Delord 26 Oct 2021 07:51

77 Abstract

78

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

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

103 Round #1

104 by Blandine Doligez, 24 Jan 2022 20:38

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

106 **Revision needed**

107

108 Dear authors,

109

110

111

112 My apologies for the delay in sending the decision.

113

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

121 R: We would like to thank the reviewers for their useful comments and the editor for allowing us to
122 resubmit a revised version of our work. We have done that revision by closely following the reviewers'
123 recommendations.

124 Further details are given below where we carefully address all major and minor concerns raised by the
125 reviewers.

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

- 128 1) the response to the reviewers,
129 2) the revised manuscript and the supplementary without the track changes
130 3) the revised manuscript and the supplementary with the track changes

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

132 Below a few additional /complementary comments:

133 - I. 26-28: the 'body-size hypothesis with respect to sex differences' is not presented before, and
134 although I can somehow figure out what this means, I think it would be good to clarify what you mean
135 here.

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

137 - I. 48: is it not 'resulting from' rather than 'resulting in'? At least here you observe the change of
138 behaviour and interpret it in terms of underlying improvement in foraging skills

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

140 - I. 52-54: I believe this is also the case in smaller species, even though this has been documented in
141 fewer cases. Some examples in passerine species that may be worth considering and citing here for
142 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>,
143 doi:10.1093/beheco/arr063,
144 <https://www.sfu.ca/biology/wildberg/NewCWEPaper/papers/BoyntonetalCondor2020.pdf>,
145 <https://ir.lib.uwo.ca/cgi/viewcontent.cgi?article=7954&context=etd>,
146 <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.2041-210x.2012.00259.x> or
147 <https://www.zora.uzh.ch/id/eprint/102335/>

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

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

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

153 - I. 136, 142, 144: is dispersal the right term here, given that the movements considered to not lead
154 to settlement for breeding? These seem to be foraging trips rather than dispersal movements.

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

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

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

160 - I. 202-205: not clear to me. Please explain

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

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

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

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

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

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

176 R: this was changed accordingly

177 - discussion: the discussion of sex differences but also molt patterns seems a bit over-detailed with
178 regards to the main objectives of the study. Not much is indeed discussed about potential sex-related
179 differences in (nor influence of molt patterns on) ontogeny of foraging behaviour. Consider shortening
180 this last part on sex differences and molt patterns, or focusing it on the differences in the dynamics of
181 behaviours with time from departure?

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

184 - also, a conclusion about the findings with regards to the ontogeny of foraging behaviour would be
185 welcome here; in particular with regards to the discussion needed about the validation of the changes
186 observed as reflecting an improvement of foraging efficiency (see reviewers' comments).

187 R: a conclusion was added in the revised version

188 - throughout the text, please check out grammar to correct mistakes /remove extra words (e.g. l.
189 379-380).

190 R: we checked carefully for grammar and mistakes

191 Reviews

192 Reviewed by Juliet Lamb, 07 Dec 2021 12:52

193 Download the review

194
195 Review: Delord et al., *The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird*
196 This study presents wet-dry patterns recorded by geolocators on Amsterdam albatrosses at different life
197 stages. The authors use these patterns to infer differences in foraging behavior among life stages, sexes,
198 and individuals. The study allows for direct comparisons between juvenile, immature, and adult life stages
199 tracked over multiple months, which is relatively unique.

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

210 in-flight vs. sit-and-wait). Thus, the results often feel repetitive, and the interpretations strained. A more
211 effective approach might be to use multivariate analysis to evaluate whether distinct foraging behaviors
212 can be detected across the various aspects of wet/dry dynamics, and then to evaluate how use of these
213 strategies varies over time and among individuals.

214 Aside from the general approach, I also had concerns about the framing of the study, analysis and
215 interpretation of results, sample sizes, and figures, which I will discuss in turn.

216 R: we warmly thank the reviewer for taking time to provide these insightful comments. Following your
217 recommendations we used a new analytical approach in the revised manuscript. First, we performed a
218 multivariate analysis by combining the five metrics obtained from the wet/dry sensor in a principal
219 component analysis. This resulted in three main independent axes that explained 94.2% of the total
220 variance and which we could easily interpret in terms of types of behaviors. This procedure ensured that
221 these three new metric (PCA axes) were independent and not correlated, therefore avoiding redundancy.
222 It also reduced the number of metrics used to describe behavior, which simplified some parts of the
223 manuscript and facilitated interpretations. In a second step, we used each of the three metrics as
224 independent variables and tested for the effects of explanatory covariates (months elapsed since
225 departure, stage, month of the year, sex) using generalized additive mixed models which considered
226 different types of random effects (no random effect, random intercept, random intercept and slope).
227 Further details are given below and in the revised manuscript. We are convinced that this new analytical
228 approach is more robust and considerably improved the quality of the manuscript, and thank you for
229 these useful suggestions.

230
231 Framing:

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

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

242
243 The authors present several unknowns in the introduction that are not tested as part of this study,
244 including whether decreased foraging efficiency contributes to juvenile mortality and which processes
245 (e.g., learned experience vs. physical development) are responsible for post-fledging changes in foraging
246 behavior. Focusing on these questions gives the misleading impression that they will be addressed in the
247 manuscript.

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

250
251 The authors emphasize the longitudinality of their study and mention multi-year data, which initially led
252 me to believe that individual results would span multiple life stages and/or years. In fact, the groups for
253 each life stage are composed of different individuals, comparison among the three groups is only possible
254 for the first 10 months post-departure, and individual trajectories are not directly mentioned or analyzed.
255 If the main goal of the paper is to make comparisons among life stages/seasons, I would suggest focusing

256 on this aspect of the work rather than on individual longitudinality; otherwise, results related to individual
257 changes over time should be presented.

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

263
264 Analysis/interpretation of results:

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

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

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

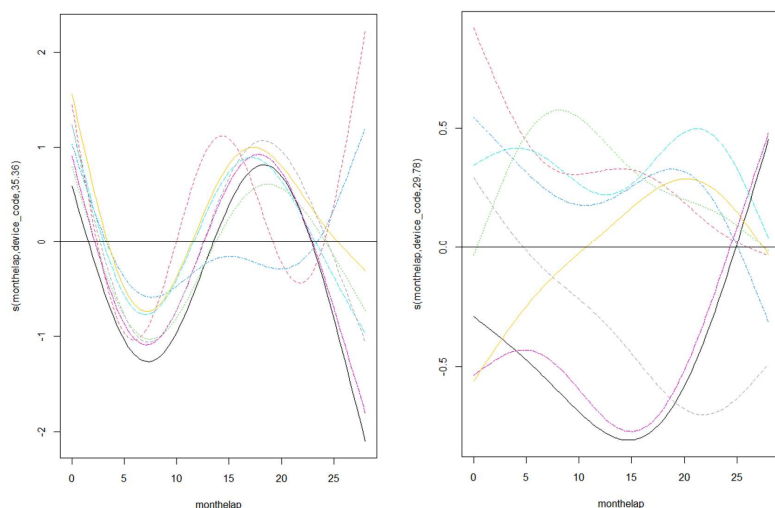
276
277 The difference in tracking duration between juveniles (2 years) and immatures/adults (1 year) also raises
278 the question of how the second year of data in tracked juveniles was treated, since behavior appears to
279 be very different during Year 2 after departure compared to Year 1. Were both years combined in other
280 analyses (e.g., month-of-year) and, if so, why? Why not present direct comparisons of Year 1 and Year 2
281 for juveniles?

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

288
289 Individual variability is mentioned in the Methods in reference to the use of mixed models, but results are
290 not presented or discussed. Given that the intercept terms in the models are significant, it seems as
291 though individual variability (i.e., specialization on different foraging strategies) could be a contributor to
292 observed variability. It would be interesting to know more about this, including whether and at what rate
293 intra-individual variation in foraging strategies decreases or stabilizes during the juvenile period (which
294 would suggest development of specialized individual foraging behaviors). Given the small sample sizes,
295 the degree of individual specialization could influence results and limit extrapolation.

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

302 departure and with random intercepts and slopes (each coloured line representing an individual) and now
303 included in the revised version supplementary (Figure S7).



304
305
306
307 Similarly, individual trajectories are not analyzed, and months since departure are treated independently
308 rather than as a continuous process. I would expect (at least in juveniles) some evolution in foraging
309 strategies over time, but the present analyses are not sufficient to detect such changes on the individual
310 level.

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

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

323
324 Although linear modeling results show significant differences in many of the tested covariates, the
325 ecological relevance of these differences appears to be relatively weak (coefficient values of <0.5 for most
326 parameters). Such differences might be expected given the large sample sizes of wet-dry bouts

327 (numbering in the thousands) and high within-individual replication. The figures also seem to show large
328 variance and high overlap among life stages across all response variables. Some discussion of effect size
329 and whether observed differences are ecologically meaningful is warranted.

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

331
332 In the text, adults and immatures are typically presented as a single group (in contrast to juveniles).
333 However, the figures and some results suggest that immatures may differ from both adults and juveniles
334 in some aspects of their behavior. It would be useful to include some discussion of these differences, and
335 of the immature life stage in general.

336 [R: following your comments analyses were changed and a paragraph was added on comparison between
337 immatures and juveniles/adults in the Discussion section L480-598](#)

338
339 The Abstract states that juvenile foraging behaviors are similar to adults within 2-3 months post-fledging,
340 while the Discussion asserts that they do not become similar until 10-17 months post-fledging. I am not
341 sure where the 10-17 months figure comes from (since direct comparisons are only possible through
342 Month 10). I assume this is related to the 15-16 month offset shown in Figure 6, but I have no idea what
343 this offset means, why it is different for adults vs. immatures, how it interacts with seasonal patterns, etc.
344 Arbitrarily comparing one aspect of adult/immature post-departure behavior to juvenile behavior more
345 than a year later does not allow for any conclusions about whether juveniles are behaving similarly to
346 adults/immatures at that time. In any case, some clarification is needed about which figure (2-3 months
347 or 10-17 months) is correct, as well as where the 10-17 month value comes from.

348 [R: following your comments this was clarified in the Abstract](#)

349
350 Sample sizes:

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

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

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

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

364 [Regarding the chronology of departure dates \(month of the year\) by stage we have the following pattern
365 \(number of individuals is indicated\):](#)

366

	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

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

370
371 Figures:

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

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

376
377 Most of the figures focus on male-female differences, while most of the discussion focuses on comparison
378 among life stages. Understanding how and whether life stages differed from one another requires
379 mentally superimposing the subfigures, which is tricky to do.

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

382
383 Minor comment: in Figure S4, the juvenile values appear to be the same in both subfigures.
384 R: thank you, the mistake was corrected and the figure modified in the revised version

385
386 Reviewed by anonymous reviewer, 23 Dec 2021 11:37
387

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

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

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

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

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

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

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

447

448 My third comment is in regard to the analyses undertaken. These complex GLMM-type analyses are not
449 my strong suit, but I do find it confusing as to why the authors assessed some models using AIC
450 comparisons and others they tested for statistical significance. As I say I am no expert, but it seems strange
451 to assess the goodness-of-fit of different models using different methods. Further, I have not come across
452 AIC comparisons between models with different response variables, is this is standard practice? If so some
453 citations to this effect would be useful. Further, I couldn't find how the authors were testing for statistical
454 significance in these models. I have seen in the past the use of likelihood ratio tests when considering
455 these complex mixed-effects models, is that what is used here? If so, I feel that this is worth including in
456 the methods, and similarly it would be nice to see some test statistics and p-values in the results section.
457 Finally, I notice in the supplementary files that some models seem to use the inverse sine square root of
458 the variable (unless I am misinterpreting $\text{asin}(\sqrt{\cdot})$ incorrectly?), yet there isn't a mention of this in the
459 main text. If this is a misinterpretation on my part, I suggest the authors might wish to amend the
460 supplementary files, and if not then they might wish to include in their manuscript a note (and perhaps a
461 citation) on why these transformations are used?

462 **R:** following your comments and those of the other reviewer we completely modified the section by
463 changing the modelling process in the revised version (please see below for detailed changes L236-330).
464 To make inferences we used model selection based on AIC comparison between competing models. Note
465 that following suggestions made by reviewer 1 we used a new analytical approach in the revised
466 manuscript. First, we performed a multivariate analysis by combining the five metrics obtained from the
467 wet/dry sensor in a principal component analysis. This resulted in three main independent axes that
468 explained 94.2% of the total variance and which we could easily interpret in terms of types of behaviors.
469 This procedure ensured that these three new metric (PCA axes) were independent and not correlated,
470 therefore avoiding redundancy. It also reduced the number of metrics used to describe behavior, which
471 simplified some parts of the manuscript and facilitated interpretations. In a second step, we used each of
472 the three metrics as independent variables and tested for the effects of explanatory covariates (months
473 elapsed since departure, stage, month of the year, sex, body size) using generalized additive mixed models
474 which considered different types of random effects (no random effect, random intercept, random
475 intercept and slope). Further details are given in the revised manuscript.
476

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

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

485

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

489 R: we thank the reviewer for the positive and constructive comments on the ms. Accordingly, we followed
490 the suggestion to modify the structure in the revised version of the ms detailed below.
491

492 Minor comments

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

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

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

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

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

504 R: this was revised accordingly throughout the Introduction section

505 Line 125: Citation needed?

506 R: citation was added (L162)

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

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

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

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

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

522 R: in our new analytical approach using generalised additive mixed models, month elapsed since
523 departure was considered as a continuous variable to investigate how individuals changed their behaviour
524 following their departure from the colony. This allowed testing for non-linear relationships. In these

525 models month of the year was used as a categorical variable with the aim of comparing how behaviors
526 differed on a seasonal basis. Although there is a correlation between these two covariates during the first
527 year, this is not the case after and according to their stage individuals do not leave the colony the same
528 month of the year (juveniles and adults leave in January and February, whereas immatures leave between
529 May and July).

530 Line 211: Visually inspected rather than tested?

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

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

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

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

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

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

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

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

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

549 Line 319: What does 'movement performance' mean?

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

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

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

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

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

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

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

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

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

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

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

578 Line 365: Cite?

579 R: reference added L661

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

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

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

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

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

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

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

592 R: according to your comments this paragraph was shorten and partly moved to the Supplementary. As
593 moulting is an important parameter which can induce behavioural changes and which has strong energetic

594 implications, we wished to keep a reduced paragraph on this theme, even if it may seem speculative
595 (L628-647; Supplementary L35-52)

596 Line 438: Perhaps include a conclusion?

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

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

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

602

603 **TITLE**

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

605 **seabird**

606

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608

609

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611

612 **Abstract**

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

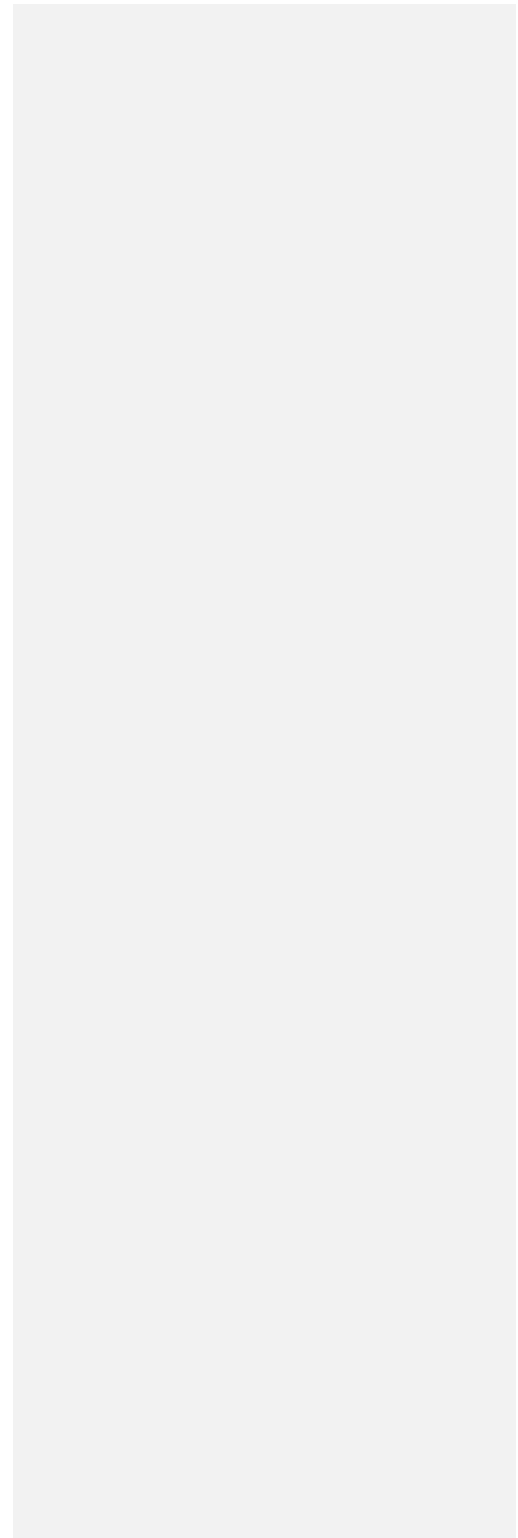
633

634

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

636 *Diomedea amsterdamensis*

637



638 **Introduction**

639 The transition from parental food dependency to independent foraging represents an important
640 developmental stage in the life cycle of most vertebrate animals (Mushinsky et al. 1982; Margrath and Lill
641 1985; Martin and Bateson 1985; Marchetti and Price 1989; Langen 1996; Burns et al. 2004) and is
642 increasingly documented in a wide range of taxa (reptiles, birds, and some mammals). A widely accepted
643 hypotheses is inadequate/inferior foraging skills of juveniles compared to adults, young naïve individuals
644 combining lack of experience and physical immaturity (Lack 1954; Daunt et al. 2007). Thus, a change in
645 behaviour, resulting from an improvement of skills acquired from increasing experience is expected to
646 occur during a period of learning through the immaturity phase. Learning often refers to stimulus-
647 response associative learning ('trial and error'; Ruaux et al. 2020), although other forms of learning (such
648 as social learning or imprinting) are also taken into account when considering the ontogeny of complex
649 behaviours (Heyes 1994; Wynn et al. 2020). Such a learning process has been studied on various taxa from
650 insects to primates (Bruner 1972; Caubet et al. 1992; Dukas 2006; Rapaport and Brown 2008).

651 Juvenile birds are known to undertake vagrant erratic journeys during the post-fledging period in
652 passerines (Naef-Daenzer and Gruebler 2008; Becker 2014; Evans 2018; Boynton et al. 2020), in raptors
653 (Urios et al. 2010; Krüger et al. 2014; Harel et al. 2016) and in seabirds (Riotte-Lambert and Weimerskirch
654 2013; Collet et al. 2020). Recent studies highlighted that the flight capacities and foraging behaviour of
655 juveniles differed from those of adults in storks (Rotics et al. 2016), raptors (Harel et al. 2016; Nourani et
656 al. 2020) or seabirds (Ydenberg 1989; Péron and Grémillet 2013; de Grissac et al. 2017; Corbeau et al.
657 2020). Most flight components were found to improve over time to tend towards those of adults (Riotte-
658 Lambert and Weimerskirch 2013; de Grissac et al. 2017; Corbeau et al. 2020).

659 However, studies focusing on the foraging behaviour of juveniles remain scarce because of the difficulty
660 to obtain individual tracking data for long periods, especially for long-lived pelagic seabirds with deferred
661 maturity. Moreover, existing studies comparing flight capacities and foraging behaviour between juveniles

662 and adults in such species only collected data during the first few months that juveniles spent at sea. Since
663 juveniles may spend several years at sea before returning to a colony to breed, our understanding of the
664 ontogeny of flight capacities and foraging behaviour remains fragmentary.

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

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

691 Previous knowledge of the ecology of large albatrosses and Amsterdam albatross described above
692 provides a practical framework for testing predictions about variability in foraging behaviour associated
693 with stage, time elapsed since departure from the colony, seasons and sex which are summarised in Table
694 S1. Given the overlap of spatial distribution between life-stages (not presented here but see Thiebot et al.
695 2014; de Grissac et al. 2016; Pajot et al. 2021) we predicted that juveniles would compensate for any lack
696 of foraging proficiency by increasing foraging effort and time (i.e. lower time spent on water and longer
697 flying bouts, in other words decreasing time sitting on water and longer and more numerous bouts in
698 flight; Hypothesis (A), Table S1). We also predicted changes in activity following fledging of juveniles from
699 the colony followed by more progressive changes. Based on results found on fledglings wandering
700 albatross (Riotte-Lambert and Weimerskirch 2013; Pajot et al. 2021) showing that juveniles reached some
701 adult foraging capacities in less than two months, we predicted that changes should be detected in activity
702 parameters early after the juvenile left the colony (within few first months). Overall, juveniles should show
703 contrasted foraging effort (i.e. longer time spent on water, shorter flying effort with fewer and shorter
704 flying bouts) just after fledging compared to other life-stages. Due to seasonal changes in food availability
705 individuals will face at sea after leaving the colony and the alleviation of energetic constraints linked to
706 reproduction (for breeding adults) or to alternate foraging trips at sea and period on land for pair bonding
707 and mating display (for immature birds), we predicted that adjustments of activity will occur according to
708 the time spent (i.e. in months elapsed) since the departure of individuals from the colony (Hypothesis (B),
709 Table S1). In juveniles, we predicted early and rapid changes after fledging and then more progressive

710 changes. Due to environmental changes occurring throughout the seasons we predicted temporal (i.e.
711 related to the month of the year) changes in activity parameters for all life-stages (Hypothesis (C), Table
712 S1). Although food availability may be lower during winter, foraging effort may also be reduced when
713 adults and immatures are moulting (Weimerskirch 1991). Molt is an intrinsically costly process requiring
714 time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual
715 replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy
716 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized albatrosses like Amsterdam albatross,
717 replacement of primary feathers lasts for more than one breeding season, and the moult of primaries
718 never occurs during the breeding season (Furness 1988; Weimerskirch 1991). Partial moulting is suspected
719 to occur outside the breeding period and to result in reduced activity (i.e. more time spent on the water;
720 Weimerskirch et al. 2015, 2020). We therefore predicted a period of reduced activity that differs according
721 to the life-stages and may be confounded by seasonal variability (Hypothesis (C). Lastly, due to sex
722 differences in flight performances (Shaffer et al. 2001; Clay et al. 2020), specifically, due to their higher
723 wing loading, males should both maintain longer flying effort, and be more likely to minimize the number
724 of flying bouts than females. Thereupon, and based on results on wandering albatross (Riotte-Lambert
725 and Weimerskirch 2013), similar pattern should be maintained outside the breeding period. We thus
726 predicted differences in foraging behaviour between sexes (i.e. time spent on water, duration and number
727 of flying and water bouts; Hypothesis (D), Table S1).

728

729 **Materials and methods**

730 **Study species and data loggers**

731 Amsterdam Island (37° 50' S; 77° 33' E) is located in the subtropical part of the southern Indian Ocean.
732 In this oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder
733 sub-Antarctic waters (Belkin & Gordon 1996). Though the diet and foraging strategy of Amsterdam

734 albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that
735 of the wandering albatross, although subtle differences can appear (Pajot et al. 2021; see Supplementary).

736 Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large
737 squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The
738 wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction
739 during the day (Nevitt et al. 2008). This strategy referred as '*foraging-in-flight*' is the lowest energy
740 consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997b). However, this
741 strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014), leading to
742 a more important utilization of the '*sit-and-wait*' technique and possibly to vary depending on sites
743 suggesting behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in
744 more frequent and shorter bouts on the water in the former technique (compared to '*foraging-in-flight*').

745 The Amsterdam albatross, like other great albatrosses, is a biennial breeder (Roux et al. 1983; Jouventin
746 et al. 1989), with high survival during juvenile, immature and adult phase (Rivalan et al. 2010). The adults
747 that raised a chick successfully do not start a new breeding cycle after chick fledging, but remain at sea
748 for a sabbatical period (~1 yr; Table 1; Rivalan et al. 2010). However, early failed breeders may start to
749 breed the following year (Rivalan et al. 2010). Immature birds may visit the colony when they are 4–7 yrs
750 old, but generally only start breeding at 9 yrs old (Table 1; Weimerskirch et al. 1997a). Juvenile birds
751 fledge and migrate independently from the adults in January (Table 1). Exact fledging dates were not
752 known for juveniles but were assessed from activity pattern as juvenile birds land on water quickly after
753 leaving the colony (Weimerskirch et al. 2006). Amsterdam albatrosses were monitored annually since
754 1983 and all individuals were individually marked (numbered stainless steel and plastic engraved colour
755 bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age (79 individuals since the
756 beginning of the study) and chicks of the year were banded, weighed (body mass \pm 50 g using a Pesola®

757 spring balance) and measured (wing length \pm 1 mm with a ruler, tarsus length, bill length, and bill depth \pm
758 0.1 mm with calipers).

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

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

781 10 min period. We used saltwater immersion to estimate daily activity budget. Despite the higher mean
782 spatial error of location estimates with these devices (over 100 km; Phillips et al. (2004a)), GLS loggers
783 allowed us to track the birds for prolonged periods with minimal disturbance to them. We considered the
784 following stages regarding the year of GLS deployment (see Table 1): juvenile, as a fledgling equipped with
785 a GLS just before leaving the colony for the first time; immature, as a non-breeding young bird that had
786 never bred equipped with a GLS when visiting the colony; adult, as a breeding adult equipped with a GLS
787 during the incubation or brooding period which successfully fledged a chick and thereafter took a
788 sabbatical year. To date, we have retrieved 40 of the 50 GLS loggers deployed in total over 4 years, from
789 which 33 individual tracks were estimated (Table 2). Our original aim was to collect activity data over the
790 three life-stages on a long period of time (>1 year). These data are available from a total of 10 adults
791 tracked throughout their sabbatical period, 13 immature birds and 10 juvenile birds (up to 3.2 years).

792

793 **Data processing**

794 The raw immersion data were obtained from testing saltwater immersion every 30 s, the GLS storing the
795 number of samples wet (> 0) at the end of each 10 min period. The data were values from 0 (no immersion
796 or dry, in flight or sitting on the ground) to 200 (permanently immersed in sea water or wet), indicating
797 the number of 3 s periods during 10 min blocks when the sensor was immersed in saltwater. Loggers
798 recorded proportion of time in seawater at 10 min intervals, which we summarized as hours in the water
799 per day (hereafter time spent on water; 10 min blocks immersion data > 0). This measure is a reliable
800 proxy of foraging effort linked to foraging behaviour of the species which enters the water principally to
801 forage (Weimerskirch and Guionnet 2002). Additionally, the duration of the bouts spent entirely
802 immersed (10 min blocks immersion data = 200) was calculated daily (hereafter referred as wet bouts
803 duration). Conversely, when birds are not on land, the time spent dry was interpreted as flying (and thus
804 not feeding). The duration of the bouts spent entirely dry (10 min blocks immersion data = 0) was

805 calculated daily (hereafter referred as dry bouts duration). Additionally the numbers of bouts (number of
806 wet bouts -sitting on water-and of dry bouts -flying) were obtained daily. Although the loggers integrated
807 activity within each 10 min block and so did not provide the exact timing of landings and take-offs, Phalan
808 et al. (2007) found for comparative purposes that bouts defined as a continuous sequence of 0 values for
809 flight (dry) and a sequence of values of 1 or greater for wet bouts, were suitable proxies for activity.
810 To select the data corresponding to periods spent at sea after leaving the breeding site, we used the
811 following criteria on activity to define the departure time from the colony for each stage: 1) juveniles, the
812 first bout spent on seawater (wet bouts duration) > 1h based on PTT tracking data (Weimerskirch et al.
813 unpublished data); 2) immatures and adults, the last bout spent flying (dry bouts duration) > 12h based
814 on PTT tracking data (Weimerskirch et al. unpublished data). Using these criteria we obtained departure
815 months as follows: 1) the juveniles fledged from the colony from January to March, 2) the immatures left
816 between April and August, and 3) the departures of sabbatical adults were spread over two periods, first
817 between December and February and then from May to July.

818

819 **Statistical analyses**

820

821 *Variation in activity parameters*

822 The aim was to determine whether distinct foraging behaviours could be detected across the patterns of
823 variation of wet/dry data, and then to appraise how these behaviours varied over time and among
824 individuals. First, to deal with the fact that wet/dry metrics were interrelated (number of wet bouts sitting
825 on water and time spent on water, wet bouts duration and dry bouts duration, wet bouts number and dry
826 bouts number) and to avoid redundancy, we ran principal components analyses (PCA built with the 'PCA'
827 function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe behaviours
828 using gradients of activity we ran PCA for i) all stages (PCS; based on activity data collected during the first

829 ten months post-departure) and for ii) juveniles only, as an additional goal was to determine changes in
830 activity patterns during the first two years of life (PCJ; based on activity data collected during the first
831 twenty-nine months post-departure).

832 Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance.
833 The first principal component (PC1S) explained 41.5% of the total variance, and correlated positively with
834 time spent on water ($r = 0.97$) and negatively with dry bouts number ($r = -0.79$). The second principal
835 component (PC2S) explained 32.5% of the variation and correlated positively with wet bouts duration (r
836 $= 0.79$) and negatively with wet bouts number ($r = -0.75$). The third principal component (PC3S) explained
837 20.2% of the variation and correlated positively with dry bouts duration ($r = 0.74$) and negatively with dry
838 bouts number ($r = -0.44$).

839 Considering juveniles, the first three principal component (PCJ) explained 92.2% of the total variance. The
840 first principal component (PC1J) explained 42.3% of the total variance, and correlated positively with time
841 spent on water ($r = 0.98$) and negatively with dry bouts number ($r = -0.76$). The second principal
842 component (PC2J) explained 32.2% of the variation and correlated positively with wet bouts duration ($r =$
843 0.72) and negatively with wet bouts number ($r = -0.75$). The third principal component (PC3J) explained
844 20.7% of the variation and correlated positively with dry bouts duration ($r = 0.48$) and negatively with dry
845 bouts number ($r = -0.46$) and wet bouts duration ($r = -0.46$).

846

847 Second, we used generalized additive mixed models (GAMMs, built with the 'gam' function, itsadug and
848 mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with each of the three first
849 axes of the PCA as the dependent variable. We separately ran models testing for variability in activity
850 parameters i) for all stages combined (PCS) and ii) for juveniles (PCJ), based on different duration of
851 datasets (28 months since departure for juveniles and 9 months since departure for immatures and adults;
852 see Supplementary; Table S2). Thus, for i) we considered the lowest number of months elapsed since

853 departure available (9 months since departure). Months elapsed since departure (the duration elapsed
854 since fledging expressed in month, i.e. the first month after fledging and so on), month of the year (i.e.
855 January and so on), sex, and stage (only for i)) were included as fixed effects.. To test for the importance
856 of individual variability in our results we built models with or without random effects. We compared
857 models without random effect, models with random intercepts, and models with random slopes and
858 intercepts to test whether the rate of change of activity parameters as a function of time elapsed since
859 departure varied between individuals (Zuur 2009a). Models included month elapsed since departure as a
860 continuous covariate modelled with non-parametric smoothing functions (Wood 2017). We limited the
861 amount of smoothing (k) with the 'gam.check' function following Wood (2017) for each spline to avoid
862 excessive flexibility and model overfitting that would have no ecological meaning. Models including all
863 combinations of explanatory variables and random effects were then tested and ranked using their Akaike
864 Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach
865 (Burnham and Anderson 2002). The model with the lowest AIC was considered as the best model. Two
866 models separated by a difference in AIC values of less than 2 were assumed to fit the data similarly.

867

868 *Variation in body size*

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

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

878

879 **Results**

880

881 *Changes in activity for all stages*

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

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

901 linked to the time elapsed since departure from the colony in the first two months after fledging
902 (Supplementary Figure S6). In immatures and adults the temporal pattern appeared reversed compared
903 to juveniles (Supplementary Figure S6).

904

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

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

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

922

923 *Body size*

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

929

930 **Discussion**

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

940

941 *Stage specific changes*

942 The birds were found to behave differently according to their stage whatever the activity variables
943 considered, indicating differences in foraging behaviour. Overall, juveniles spent lower percentage of time
944 on water compared to immatures and adults. Nonetheless, during the first month following their
945 departure from the colony while the proportion of time spent on water by immatures and adults showed
946 a dome-shaped curve peaking three to five months after departure, juveniles changed abruptly, with
947 values dropping off in the first two months and then remaining low and overall lower than in adults and

948 immatures. This might indicate a lower foraging activity in naïve birds. During the same period, the
949 duration and number of water bouts also exhibited progressive change. These patterns suggest an early
950 and gradual change in foraging behaviour and that juveniles progressively behaved similarly to immatures
951 and adults (reaching similar values in activity covariates). It is noteworthy that the multi-monthly bell-
952 shaped pattern observed during the first 10 months after departure in immatures and adults appears to
953 be mirrored in juveniles 15-16 months later (see Figure S12). Together, these results suggest a progressive
954 behavioural change in movements during the first two months after fledging. This seems to indicate that
955 juvenile individuals may have weaker foraging skills during their first two months at sea. Although
956 behavioural changes can often equate to improved performance (e.g. Campioni et al. 2020) this is not
957 always the case. The emergence of juvenile birds as more '*adult like*' in their foraging/flight behavioural
958 patterns is not necessarily a sign of improvement.

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

970 Since all stages of the Amsterdam albatross forage in the same water masses (see Thiebot et al. 2014),
971 differences in foraging behaviour were presumably not due to different oceanographic characteristics as

972 observed in other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al. 2020b). These lower
973 performances could be due to a combination of lack of experience of optimal behaviours, poor knowledge
974 of the environment, use of distinct cues and/or physical immaturity (Shaffer et al. 2001; Frankish et al.
975 2020a, 2022). It is likely that increasing exposure to diverse foraging situations allows juveniles to rapidly
976 accumulate foraging experience and improve various aspects of foraging.

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

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

996

997 *Temporal changes in activity*

998 The temporal variability of activity was found whatever the life-stage considered. Part of the activity
999 changes observed following the departure of juveniles Amsterdam albatross may illustrate the swift
1000 change in travel and movement behaviour, reflecting a more '*adult like*' behaving, not indicating
1001 necessarily an improvement of flight performances and of the ability to cope with changing (i.e. increasing
1002 wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such as albatrosses.
1003 Both extrinsic (i.e. environmental conditions: variability in subtropical waters resources or in wind) and
1004 intrinsic (i.e. energetic demands linked to plumage renew) factors could be involved in the modulation of
1005 foraging behaviour, which can be reflected in the temporal variability. Subtropical environments in the
1006 southern Indian Ocean are generally characterized as oligotrophic areas but nonetheless are known to
1007 vary over the seasons. During the austral winter, colder surface waters and strong winds result in changes
1008 of oceanographic conditions associated with an increased primary productivity (Behera and Yamagata
1009 2001; Terray 2011; Delord et al. 2021). Changes in water temperature associated with wind appear to
1010 result in seasonal biological production variations that affect seabirds (Delord et al. 2021).

1011 In seabirds, temporal changes in foraging activities are often associated to the very strong contrast
1012 between reproduction and inter-breeding periods, shifting from high energetic needs linked to
1013 reproductive effort and associated constraints (i.e. central place foraging strategy; Orians and Pearson
1014 1979) to a reduction of these energetic constraints during the non-breeding period (sabbatical year for
1015 adults) (Williams 1966; Ricklefs 1977, 1983; Stearns 1992; Ydenberg et al. 1992). This contrast is
1016 particularly pronounced in seabirds (Mackley et al. 2010; Gutowsky et al. 2014) where energetic
1017 constraints play a decisive role in determining activity patterns (Phalan et al. 2007).

1018 Molt is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996;
1019 Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in

1020 both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). Stage-specific
1021 and sex-specific differences in moult extent occur in wandering albatross, suggesting important
1022 constraints (Weimerskirch 1991; see Supplementary). Recently Gutowsky et al. (2014) suggested that
1023 tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could
1024 compromise flight from active wing moult during the non-breeding period and induce changes in daily
1025 activity budget during a 'quasi-flightless' stage. However, there is no such data for southern albatrosses.
1026 Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested
1027 it such a compromise. However, adult birds during the non-breeding season appear to spend much more
1028 time on the water during winter, suggesting that partial moult may occur at this time, as observed in many
1029 other seabird species that have to moult during the non-breeding season and show reduced activity during
1030 specific periods that may correspond to moulting (Weimerskirch et al. 2015b, 2020). Interestingly,
1031 immature appear to have this peak in time spent on the water in spring, suggesting different timing of
1032 moult.

1033

1034 *Sex differences in activity*

1035 Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross
1036 forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013;
1037 Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by
1038 differences in foraging habitats. We found support for the body-size hypothesis to explain sex differences
1039 in activity parameters, consistent with the important sexual dimorphism in the Amsterdam albatross.
1040 Males did more bouts on water whatever the stage, and depending on stage, shorter (juveniles only)
1041 compared to females. Consistently, we found that males flew for longer periods (dry bouts duration)
1042 compared to females. When considering all stages, males spent a higher percentage of time on water
1043 compared to females.

1044 Amsterdam albatross and its sister species the wandering albatross have a very close anatomy and similar
1045 use of the wind, although Amsterdam albatross is 5-8% smaller and 25% lighter (Barbraud et al.
1046 unpublished data. In the wandering albatross, due to sex differences in flight performance (specifically,
1047 due to their higher wing loading), males should both maintain longer flying effort and be more likely to
1048 minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). The change in
1049 foraging strategy, as in wandering albatross, tends to be dependent on breeding stage (Phalan et al. 2007;
1050 Louzao et al. 2014) leading to a greater use of the '*sit-and-wait*' technique and may vary between sites,
1051 suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques
1052 could result in more frequent and shorter bouts on the water in the '*sit-and-wait*' technique (compared
1053 to '*foraging-in-flight*'). In other word, males may have more of a '*sit-and-wait*' strategy while females have
1054 more of a '*foraging-in-flight*' strategy, although there is some behavioural plasticity particularly over time.
1055 Our prediction that foraging behaviour differs between sexes was fully supported (i.e. sex-differences in
1056 activity parameters). Nevertheless, the similarity in time spent on the water suggests that the differences
1057 may be more subtle, showing some a trade-offs in duration and numbers between flying and water bouts.
1058 This trade-off should vary depending on stage as immature females tended to have shorter and more
1059 frequent bouts on the water. This implies that while probably feeding on similar water masses, the sexes
1060 might differ in type of prey targeted and/or used different foraging methods. The confirmation of this
1061 hypothesis reinforces the fact that the two-sibling species, as previously assumed, show a high degree of
1062 similarity in their foraging behaviour.

1063 Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex
1064 usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can
1065 result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey
1066 (Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019;
1067 Barbraud et al. 2021). It has also been suggested that size matters probably because the smaller and

1068 lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower
1069 wing loaded female wandering albatrosses, compared to males, are probably better able to exploit
1070 subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that
1071 females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than
1072 males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al.
1073 (2002); Stauss et al. (2012)).

1074

1075 *Individual variability in activity*

1076 There was inter-individual variability in almost all activity parameters whatever the stage considered. In
1077 juveniles, models indicated inter-individual variability in activity and in the rate of change of activity as a
1078 function of time elapsed since departure from the colony. Since the intercept terms in the models were
1079 significant, it seems as though individual variability (i.e., specialization on different foraging strategies)
1080 was a contributor to observed variability. However, the rate of change of intra-individual variation for
1081 some foraging strategies (percentage of time on water-number of flying bouts axis) oscillated during the
1082 juvenile period with a seemingly remarkable synchrony (see Fig S7). This suggests that changes in foraging
1083 behaviours occurred at the individual level during the juvenile period without stabilizing, at least during
1084 the first two years after fledging. This individual variability suggests development of specialized individual
1085 foraging behaviours (Harel et al. 2016; Rotics et al. 2016, 2021; Phillips et al. 2017). Nonetheless, given
1086 the small sample sizes these results should be interpreted with caution.

1087

1088 **Conclusion**

1089 Very few studies have investigated the ontogeny of foraging behaviour over such a long period of time,
1090 particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over
1091 several years. We investigated the foraging behaviour, through activity patterns, during the three life

1092 stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naïve juveniles,
1093 immatures and adults. Naïve juveniles during their first month at sea after leaving their colony exhibited
1094 lower foraging activity (greater proportion of time spent sitting on water, longer and more numerous
1095 bouts on water, and shorter and fewer flying bouts). Patterns of activity parameters in juveniles after
1096 independence suggested a progressive change of foraging performances during the first two months since
1097 fledging. Regardless of life stage considered, activity parameters exhibited temporal variability reflecting
1098 the modulation of foraging behaviour presumably linked to both extrinsic (i.e. environmental conditions
1099 such as variability in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage
1100 renew during moult) factors. Sex differences in activity parameters according to time since departure from
1101 the colony and season were consistent with the sexual dimorphism in the Amsterdam albatross. It is
1102 therefore expected that a change in behaviour, resulting from the experience gained, may reflect an
1103 improvement in skills occurring during a period of learning through the immaturity phase.

1104

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1116 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	1 st 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 <i>t</i> to the following 15 January year <i>t+1</i>)	~8-28 years	~1 year	Breeding adults at the end of reproductive cycle and leave the colony to forage at sea

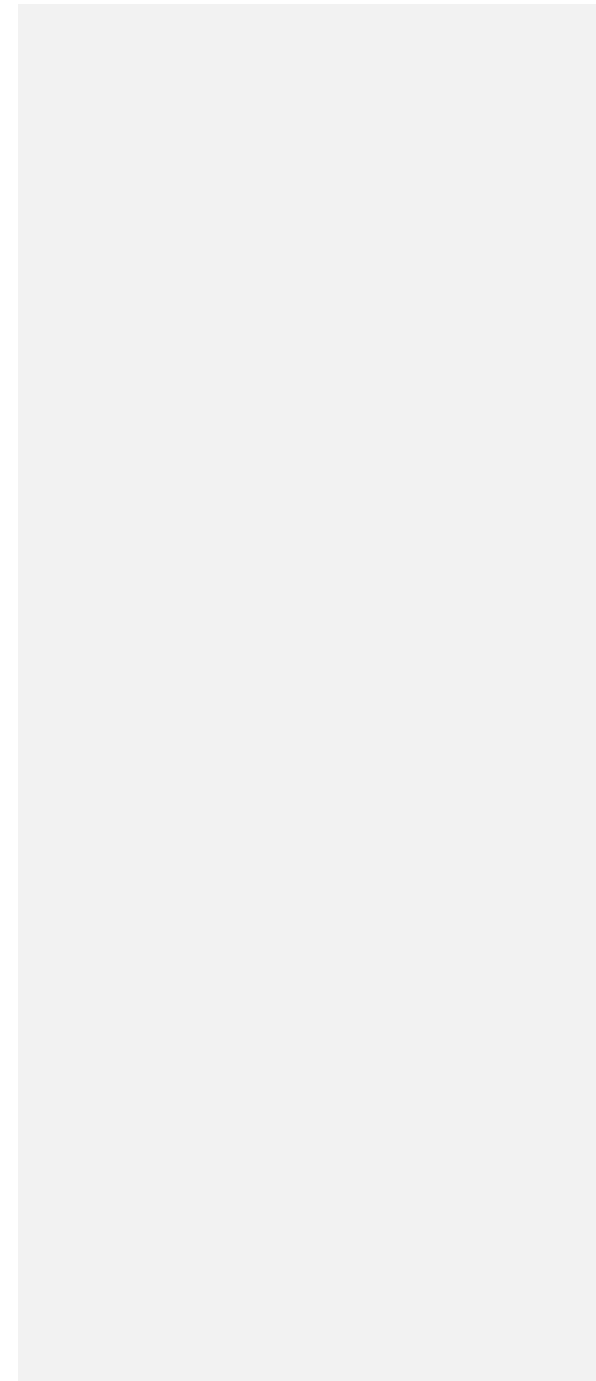
1117 ¹ Stage/Age at which the individuals were equipped with loggers in our study

1118 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 (<i>t</i> +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)

1119 ¹ number of females F and males M, or not known NK for each stage

1120



1121 Table 3 Model selection for variations in activity parameters of Amsterdam albatrosses in relation to sex, stage, number of months spent since
 1122 departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the
 1123 year (i.e. January and so on)

Models	Fixed effects	Random effects	AIC	Δ AIC
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

1124 Models are ranked according to decreasing statistical support, as indicated by AICc. The first best models are shown

1125 Table 4 Values of activity parameters (mean \pm sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam

1126 albatross

1127

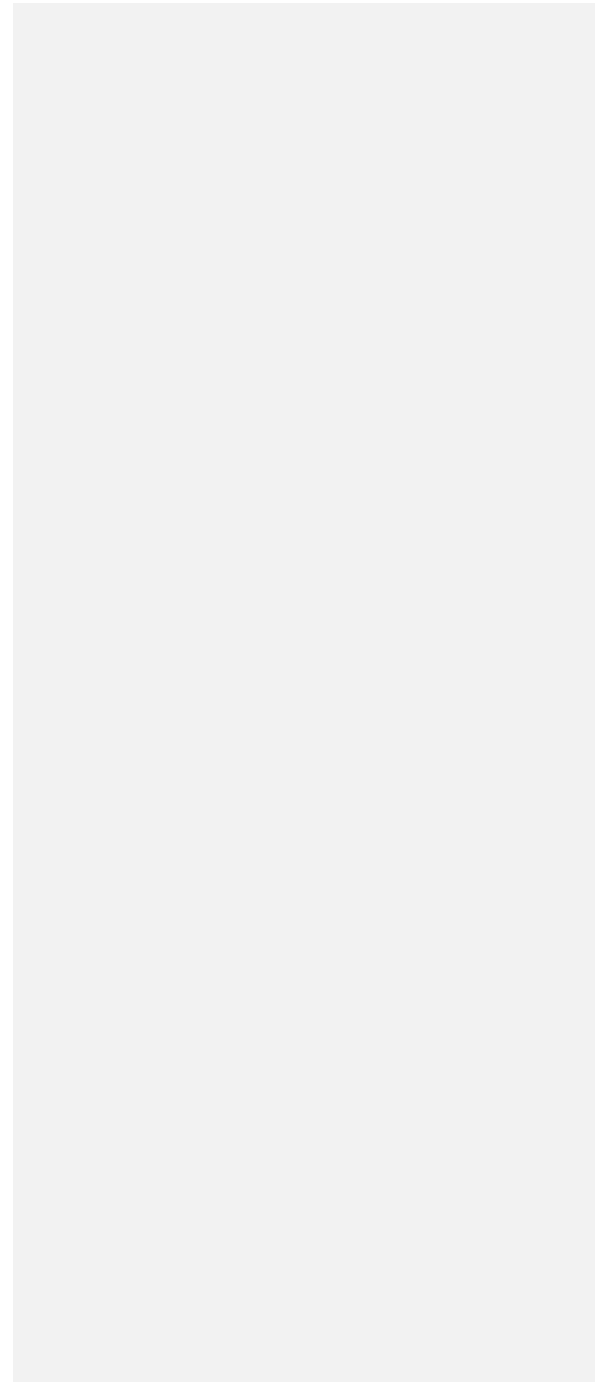
	Juvenile ¹		Juvenile ²		Immature		Adult sabbatical	
	female	male	female	male	female	male	female	male
Time spent on water (%)	55.04 \pm 20.46	58.18 \pm 21.11	51.41 \pm 19.18	52.88 \pm 20.39	59.25 \pm 21.53	63.31 \pm 21.17	64.89 \pm 20.90	69.98 \pm 18.10
Wet bouts (sitting on water) duration (h)	1.21 \pm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

1128 ¹ calculated during 28 months following departure; ² calculated during 9 months following departure

1129 Table 5 Model selection for variations activity parameters for juveniles Amsterdam albatrosses in relation to sex, number of months spent since
 1130 departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the
 1131 year (i.e. January and so on)

Models	Fixed effects	Random effects	AIC	Δ AIC
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



1133 Table 6 Body measurements of juveniles and adults Amsterdam albatross and percentage of differences between sexes for each measurement. Δ

1134 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 \pm 62.1	543.6 \pm 72.5	637.0 \pm 13.3	654.7 \pm 14.7	2.1	2.7	1.021	1.026	W=10554 P<0.01	t₆₄=-4.882 p<0.001
Tarsus length (mm)	113.1 \pm 3.8	118.4 \pm 3.8	112.4 \pm 3.9	116.4 \pm 4.0	4.5	3.5	1.047	1.077	t₂₂₉= -10.54 p<0.001	t₂₈= -3.982 p<0.001
Bill length (mm)	137.1 \pm 4.0	143.1 \pm 3.8	140.9 \pm 4.7	145.0 \pm 3.5	4.2	2.8	1.044	1.034	t₃₁₉= -13.89 p<0.001	t₇₂= -4.268 p<0.001
Bill depth (mm)	34.8 \pm 3.4	36.9 \pm 3.4	36.0 \pm 1.5	38.0 \pm 1.5	5.8	5.2	1.061	1.000	t₃₁₈= -5.629 p<0.001	t₅₈= -4.821 p<0.001
Body mass (g)	7719 \pm 1228	8859 \pm 1546	7509 \pm 1561	7257 \pm 1207	12.9	3.4	1.148	1.077	t₁₉₃=-5.846 p<0.001	t₃₂=0.512 p=0.612

1135 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
 1136 (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
 1137 test)

1138 Table 7 Selected generalized linear models testing for the effect of sex and stage on body measurements
 1139 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

1140

1141 Table 8 GLM results for wing length of Amsterdam albatross modelled as a function of sex and stage
 1142 (GLM1). 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

1143

1144 Table 9 GLM results for tarsus length of Amsterdam albatross modelled as a function of sex and stage
 1145 (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

1146 Table 10 GLM results for bill length of Amsterdam albatross modelled as a function of sex (GLM3).

1147 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

1148

1149 Table 11 GLM results for bill depth of Amsterdam albatross modelled as a function of sex (GLM4).

1150 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

1151

1152 Table 12 GLM results for body mass of Amsterdam albatross modelled as a function of sex and stage

1153 (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

1154

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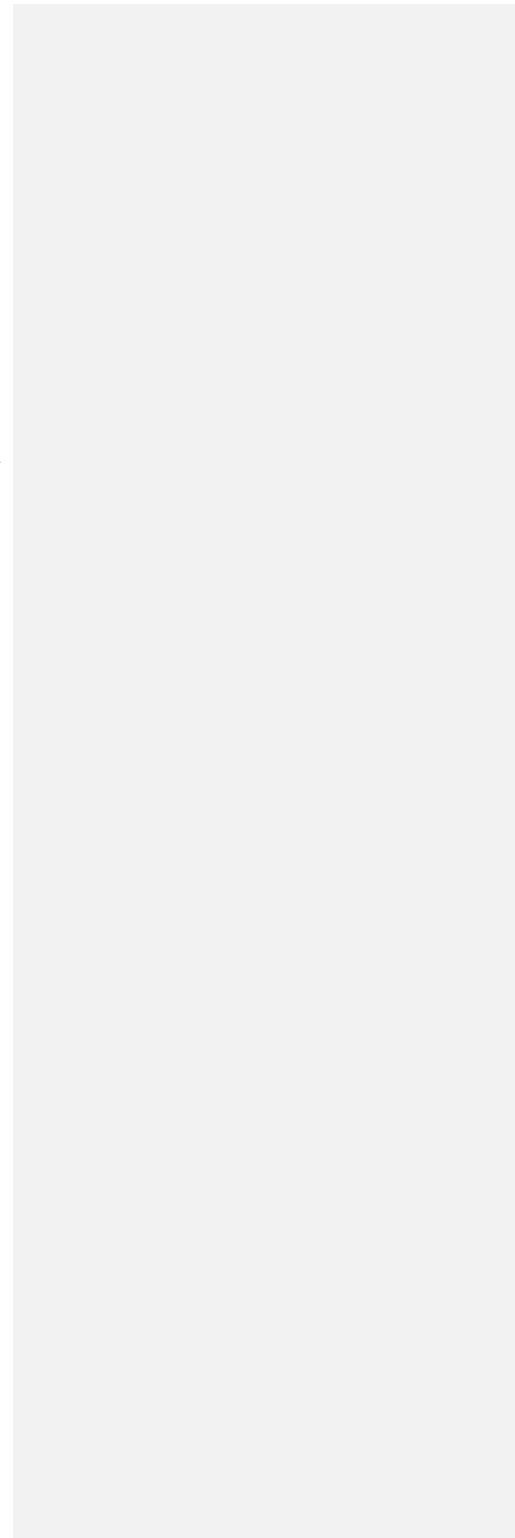
1156 **FIGURES**

1157 Figure 1 Modeled a) first and b) second axis of principal components analysis of activity parameters of all
1158 stages (i.e. adult, immature and juvenile) of Amsterdam albatrosses according to time elapsed (e.g.
1159 duration elapsed since departure from the colony expressed in month). Plain line corresponds to
1160 estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval.

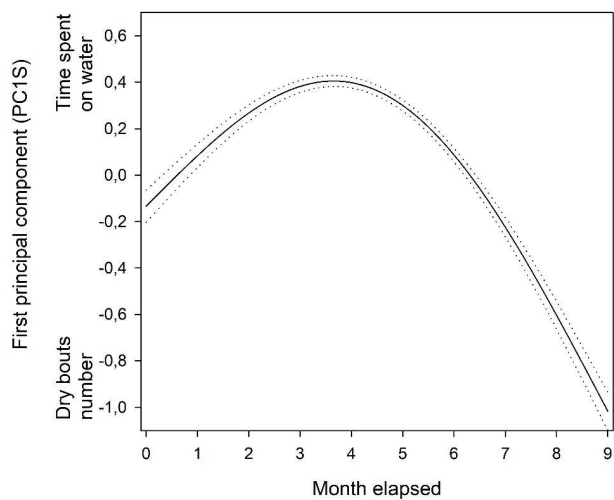
1161

1162 Figure 2 Modeled a) first and b) second axis of principal components analysis of activity parameters of
1163 juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from
1164 the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model.
1165 Dotted lines indicate 95% confidence interval.

1166

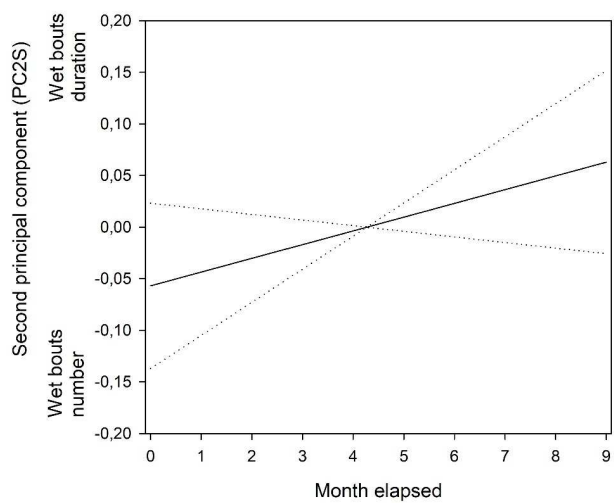


1167 Figure 1a



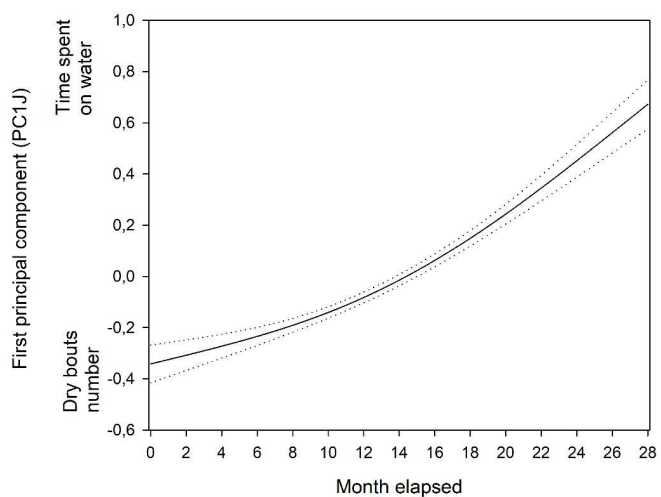
1168

1169 Figure 1b



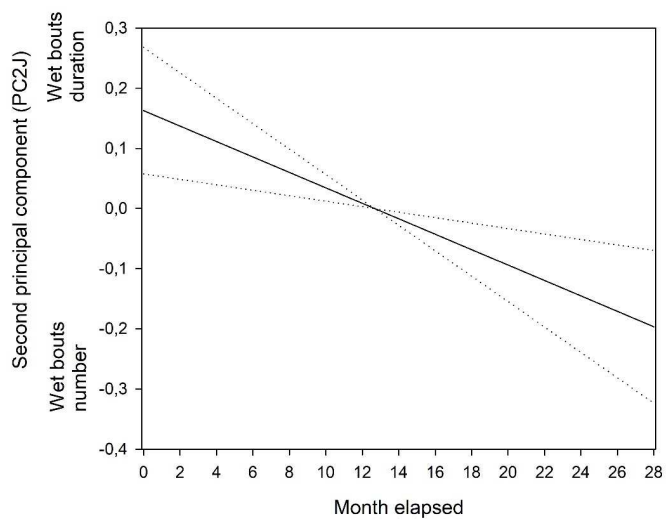
1170

1171 Figure 2a



1172

1173 Figure 2b



1174

1175 **The authors of this article declare that they have no financial conflict of interest with the content of**
1176 **this article.**

1177

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1418
1419

1420 **Supplementary**

1421

1422 **Species biological aspects**

1423 Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to
1424 have very similar foraging behaviour compared to that of the wandering albatross, although subtle
1425 differences can appear (Pajot et al. 2021). Like other large albatross species (*Diomedea spp.*), the
1426 Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et
1427 al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive
1428 distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred
1429 as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the wandering albatross
1430 (Weimerskirch et al. 1997). However, this strategy tends to change depending on breeding stage (Phalan
1431 et al. 2007; Louzao et al. 2014) leading to a more important utilization of the '*sit-and-wait*' technique and
1432 possibly to vary depending on sites suggesting considerable behavioural plasticity (Phalan et al. 2007).
1433 This switch in foraging techniques could result in more frequent and shorter bouts on the water in the
1434 former technique (compared to '*foraging-in-flight*').

1435 Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical
1436 period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale migratory movements
1437 reaching >4000 km from the colony exploiting continuously warm waters (~18°C). No clear longitudinal
1438 seasonality existed in the movements of adults, nonetheless they tended to move westwards in June/July
1439 and eastwards in November. The immature birds moved widely in longitude (0° to 135° E), exploiting
1440 exclusively warm waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity
1441 existed in the movements, except that they also tended to move westwards in June and eastwards in
1442 November. Juveniles exhibited very large post-fledging movement capacities over the southern Indian
1443 Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal

1444 gradient (27° to 47° S). Juveniles birds tended to move westwards first in March-April and temporarily
1445 exhibited synchronous individual movements. De Grissac et al. (2016) compared trajectories (i.e.
1446 departure direction or orientation toward specific areas) of juveniles and adults and showed that juveniles
1447 performed an initial rapid movement taking all individuals away from the vicinity of their native colony,
1448 and in a second time performed large-scale movements similar to those of adults during the sabbatical
1449 period. High individual variability and no clear differences between juveniles and adults patterns were
1450 found, except that adults foraged at significantly higher latitudes. De Grissac et al. (2016) concluded in an
1451 overlap in distribution between adults and juveniles due to the extensive area they used and their
1452 differences in latitudinal distribution compared to other Procellariiformes species.

1453
1454 Moulting is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996;
1455 Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in
1456 both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized
1457 albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding
1458 season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch
1459 1991). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting
1460 important constraints that could compete with breeding (immature birds tend to renew fewer feathers
1461 compared to adult breeders), and particularly in females (Weimerskirch 1991). In smaller sized seabirds,
1462 a link between moulting pattern and activity parameters was evidenced, resulting in a clear temporal
1463 pattern partly explained by moult (Cherel et al. 2016). Recently Gutowsky et al. (2014) suggested that
1464 tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could
1465 compromise flight from active wing moult during the nonbreeding period and induce changes in daily
1466 activity budget during a 'quasi-flightless' stage. However, there is no such data for southern albatrosses.
1467 Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested

1468 it such a compromise. However, adult birds during the non-breeding season appear to spend much more
1469 time on the water during winter, suggesting that partial moult may occur at this time, as observed in many
1470 other seabird species that have to moult during the non-breeding season and show reduced activity during
1471 specific periods that may correspond to moulting (Weimerskirch et al. 2015, 2020).

1472 Table S1 Hypotheses and predictions about the factors driving differences in activity (time spent on water, number and duration of flying bouts,
 1473 number and duration of water bouts) year-round in Amsterdam albatrosses
 1474

Hypothesis	Predictions		
	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	<p>Adults/immatures: two-periods pattern including one with lowering activity</p> <p>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</p> <p>Following departure from the colony adjustment in foraging effort or moult constraints</p>	<p>Adults/immatures: two-periods pattern including one with lowering activity</p> <p>Juveniles: change in foraging skills corresponding to gradual change with increasing flying bouts duration and number during the 1st months after fledging</p> <p>Adjustment in foraging effort or moult constraints according to time elapsed since departure</p>	<p>Adults/immatures: two-periods pattern including one with lowering activity</p> <p>Juveniles: change in foraging skills corresponding to gradual change with decreasing water bouts duration and number during the 1st months after fledging</p> <p>Adjustment in foraging effort or moult constraints according to time elapsed since departure</p>
(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

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

Alternative prediction: no specific prediction due to trade-off between duration and number of bouts

1476 Table S2 Selected models testing for the effects of sex, stage, number of months spent since departure (monthelap: duration elapsed since fledging
 1477 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
 1478 Amsterdam albatrosses

	Model #	Study variable ¹	Model structure	Sample size
All stages	gamm1	PC1S	$\sim s(\text{monthelap}, k = 2) + \text{monthf} + \text{stade} + \text{sex} + s(\text{monthelap}, \text{device_code}^2, \text{bs} = \text{"re"})$	8094
All stages	gamm2	PC2S	$\sim s(\text{monthelap}, k = 3) + \text{monthf} + \text{stade} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"})$	8094
All stages	gamm3	PC3S	$\sim \text{monthf} + \text{stade} + \text{sex} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"})$	8094
Juveniles	gamm4	PC1J	$\sim s(\text{monthelap}, k = 2) + \text{monthf} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"})$	6161
Juveniles	gamm5	PC2J	$\sim s(\text{monthelap}, k = 2) + \text{monthf} + \text{sex} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"})$	6161
Juveniles	gamm6	PC3J	$\sim \text{monthf} + \text{sex} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"})$	6161

1479 ¹ First, second and third principal component issued from principal components analyses considering i) all stages combined (PCS) and ii) only

1480 juveniles (PCJ); ² Individuals

1481 Table S3a GAMM results for the first principal components (PC1S; gamm1 see Table S2) of Amsterdam
 1482 albatross modelled as a function of months spent since departure from the colony (monthelap), month
 1483 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

1484

	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

1485

1486

1487 Table S3b GAMM results for the second principal components (PC2S; gamm2 see Table S2) of
 1488 Amsterdam albatross modelled as a function of months spent since departure from the colony
 1489 (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

1490

	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

1491

1492

1493 Table S3c GAMM results for the third principal components (PC3S; gamm3 see Table S2) of Amsterdam
 1494 albatross modelled as a function of months spent since departure from the colony (monthelap), month
 1495 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

1496

	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

1497

1498

1499 Table S4a GAMM results for the first principal components (PC1J; gamm4 see Table S2) of juveniles
 1500 Amsterdam albatross modelled as a function of months spent since departure from the colony
 1501 (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

1502

	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

1503

1504

1505 Table S4b GAMM results for the second principal components (PC2); gamm5 see Table S2) of juveniles
 1506 Amsterdam albatross modelled as a function of months spent since departure from the colony
 1507 (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

1508

	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

1509

1510

1511 Table S4c GAMM results for the third principal components (PC3); gamm5 see Table S2) of juveniles

1512 Amsterdam albatross modelled as a function of months spent since departure from the colony

1513 (monthelap), month of the year and sex. Reference value are January and females.

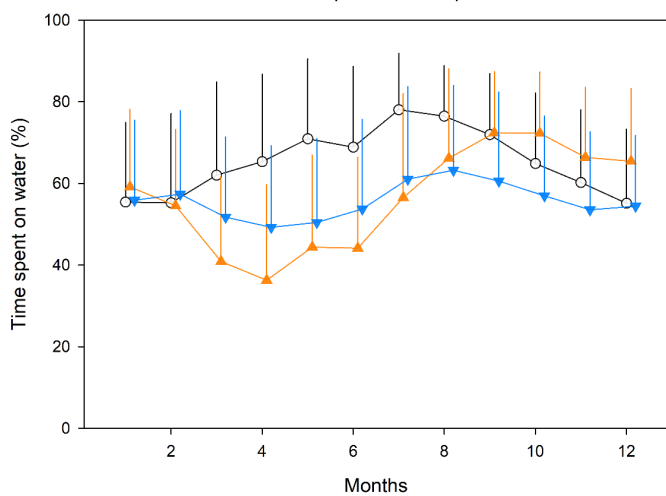
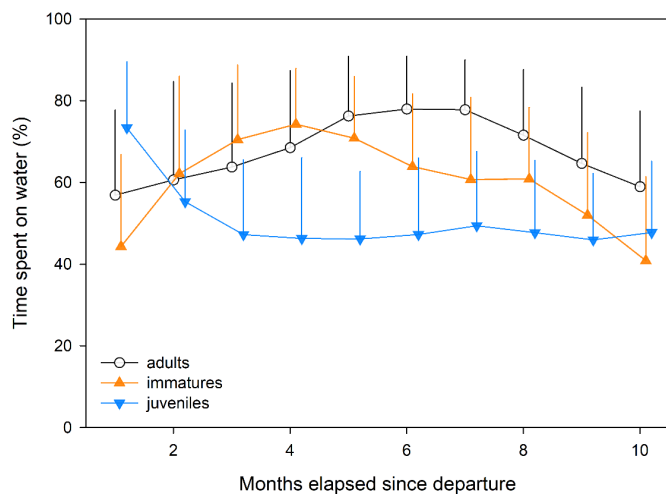
Variable	Smoother edf	F-test	p-value
s(monthelap,device_code)	7.724	19.37	0.000

1514

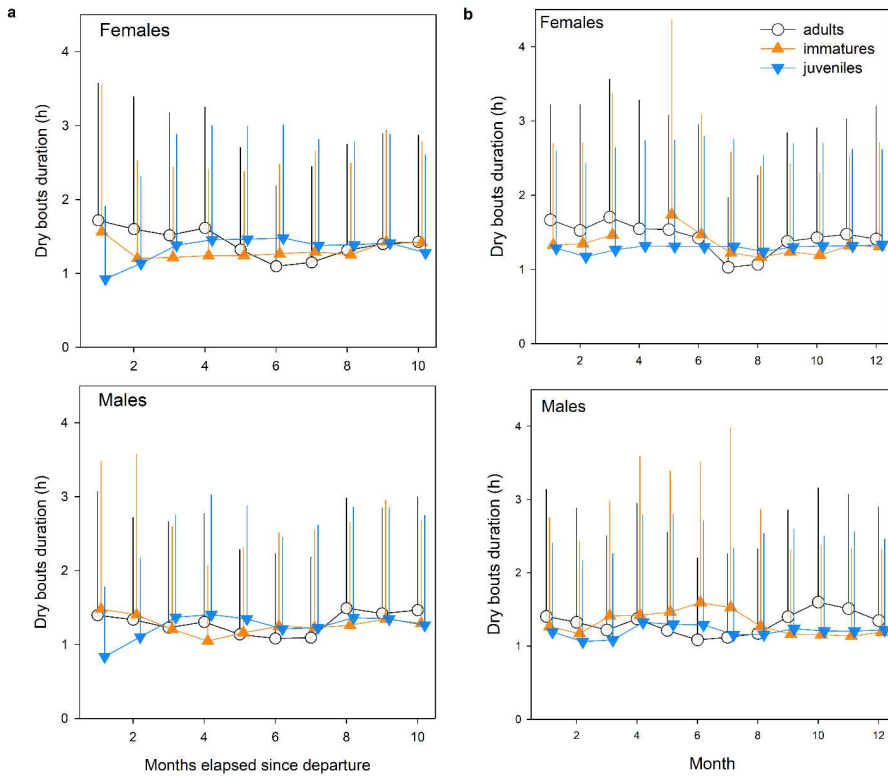
	Estimate	Std.Error	t-value	p-value
(Intercept)	-0.04	0.05	-0.77	0.444
February	-0.10	0.06	-1.59	0.113
March	-0.13	0.06	-2.19	0.029
April	-0.06	0.06	-0.94	0.349
May	0.02	0.06	0.37	0.715
June	0.13	0.06	2.11	0.035
July	0.02	0.06	0.25	0.802
August	0.00	0.06	0.01	0.992
September	0.00	0.06	0.01	0.996
October	-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

1515

1516 FIGURES

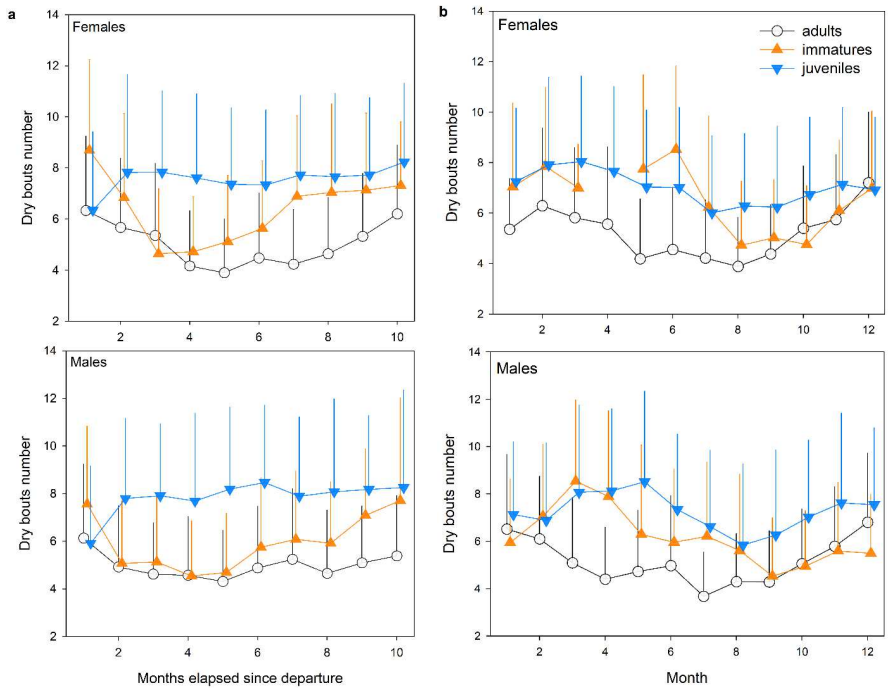


1517
1518 Figure S1 Daily proportions of time spent on water depending on stage (juveniles, immatures and adults)
1519 for every month since departure from the colony (upper panel) and for each month of the year (lower
1520 panel). Error bars represent ± 1 sd



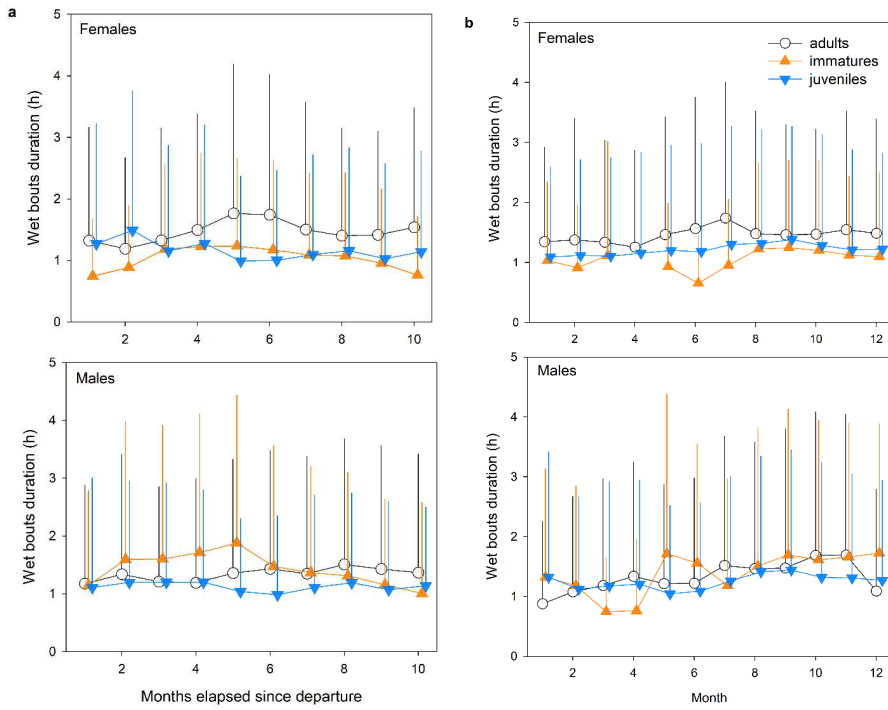
1521

1522 Figure S2 Daily flying bouts duration (dry bouts in hours) depending and on sex (females and males) and
 1523 on stage (juveniles, immatures and adults) for a) time elapsed since departure from the colony expressed
 1524 in month (left panel) and for b) each month of the year (right panel). One side error bars represent ± 1 sd



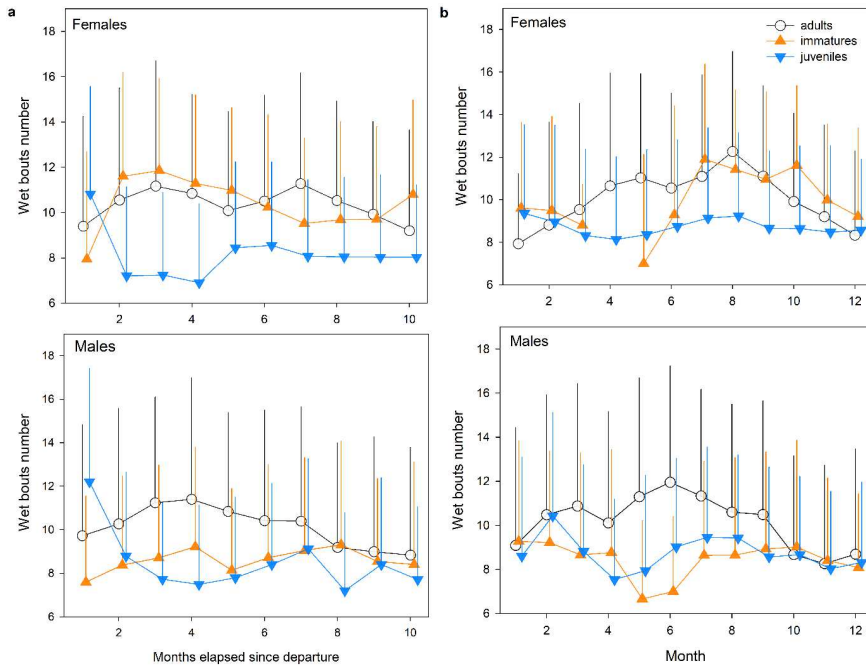
1525

1526 Figure S3 Daily flying bouts number (dry bouts) for every month since departure from the colony for
 1527 juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent
 1528 ± 1 sd



1529

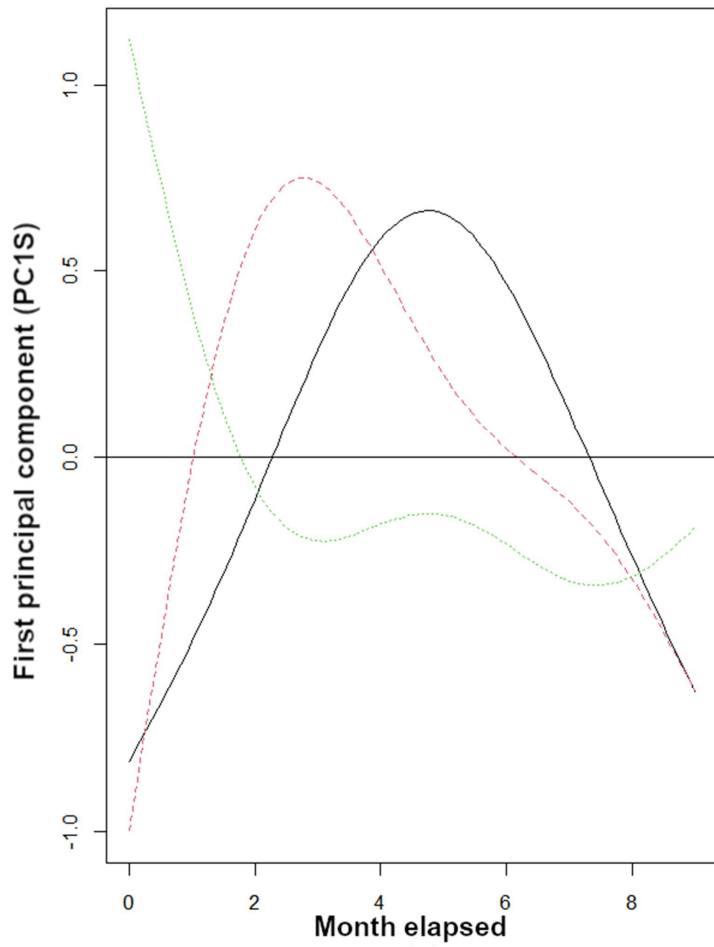
1530 Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures
 1531 and adults) and on sex (females and males) for every month since departure of the colony (upper panel)
 1532 and for each month of the year (lower panel). Error bars represent ± 1 sd



1533

1534 Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for
 1535 juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent
 1536 ± 1 sd

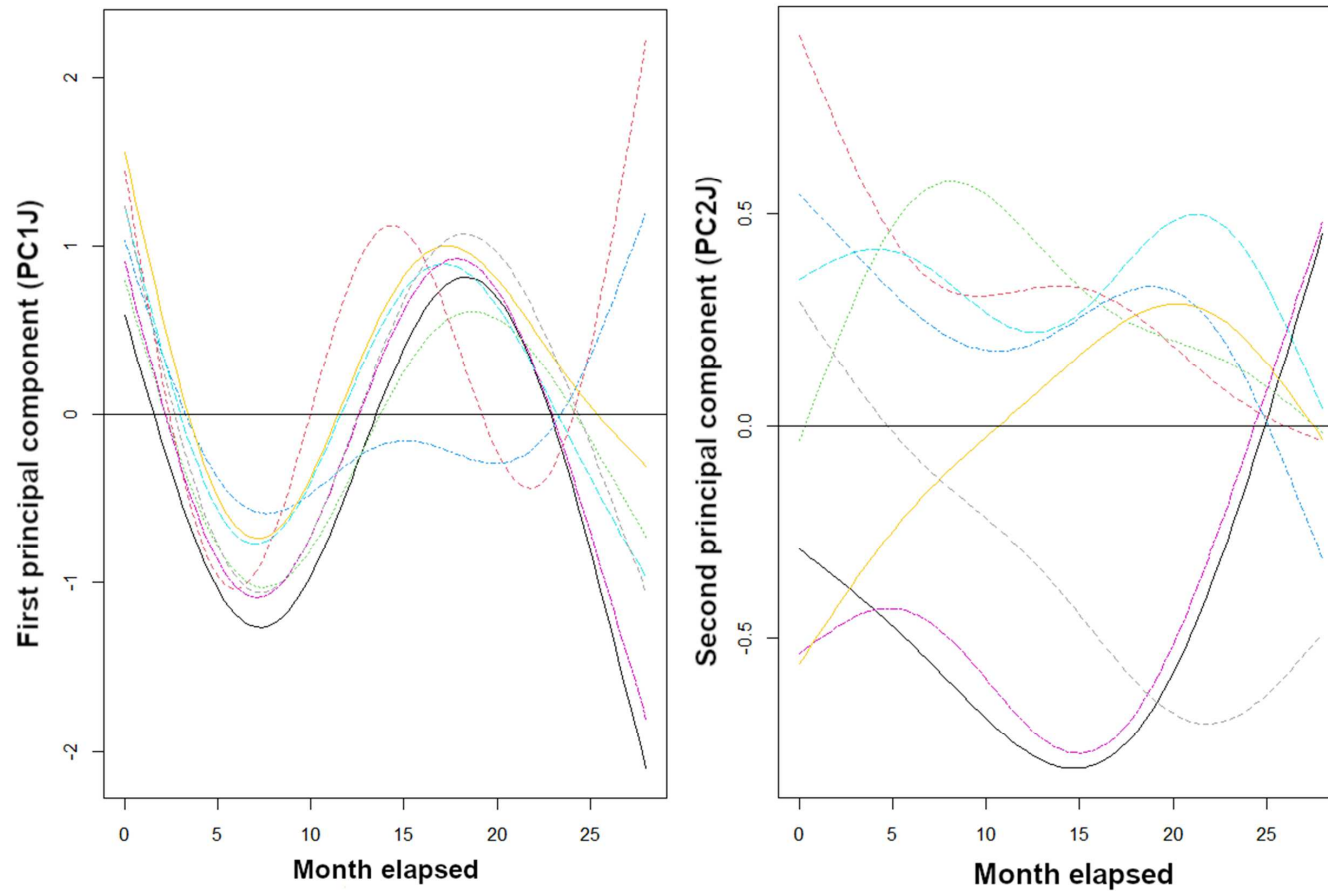
1537



1538

1539 Figure S6 Modeled first axis of principal components analysis of activity parameters of all stages (i.e. adult
 1540 (plain black line), immature (dashed red line) and juvenile (dotted green line)) of Amsterdam albatrosses
 1541 according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month).
 1542 Plain line corresponds to estimated smoother from the GAMM model

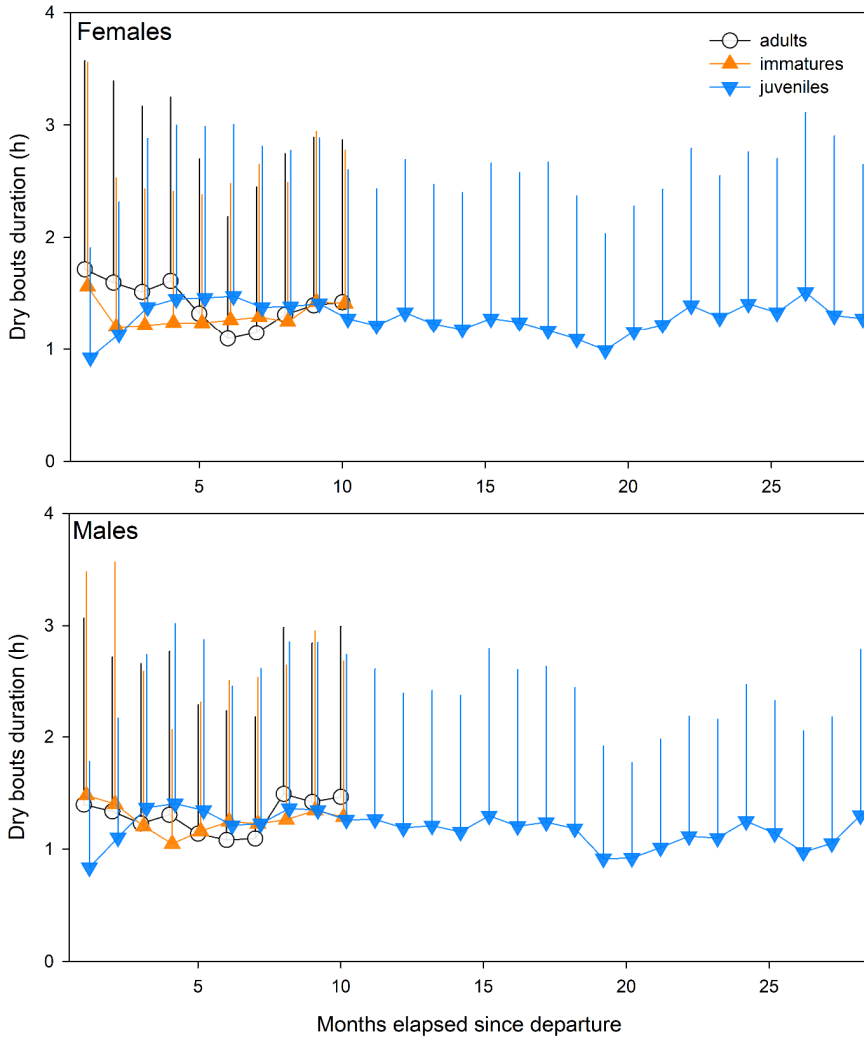
1543



1544

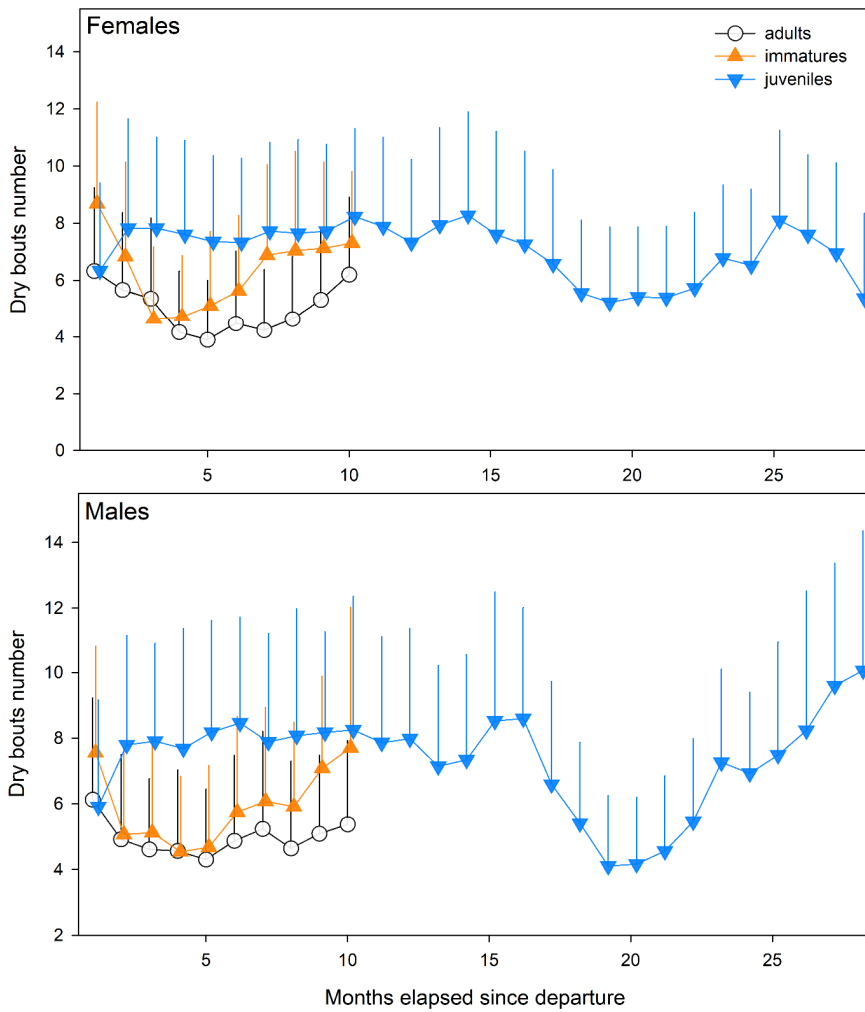
1545 Figure S7 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of Amsterdam
 1546 albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs obtained using
 1547 random intercepts and slopes (each coloured line representing an individual). Line corresponds to estimated smoother from the GAMM models

1548



1549

1550 Figure S8 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony
1551 for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars
1552 represent ± 1 sd



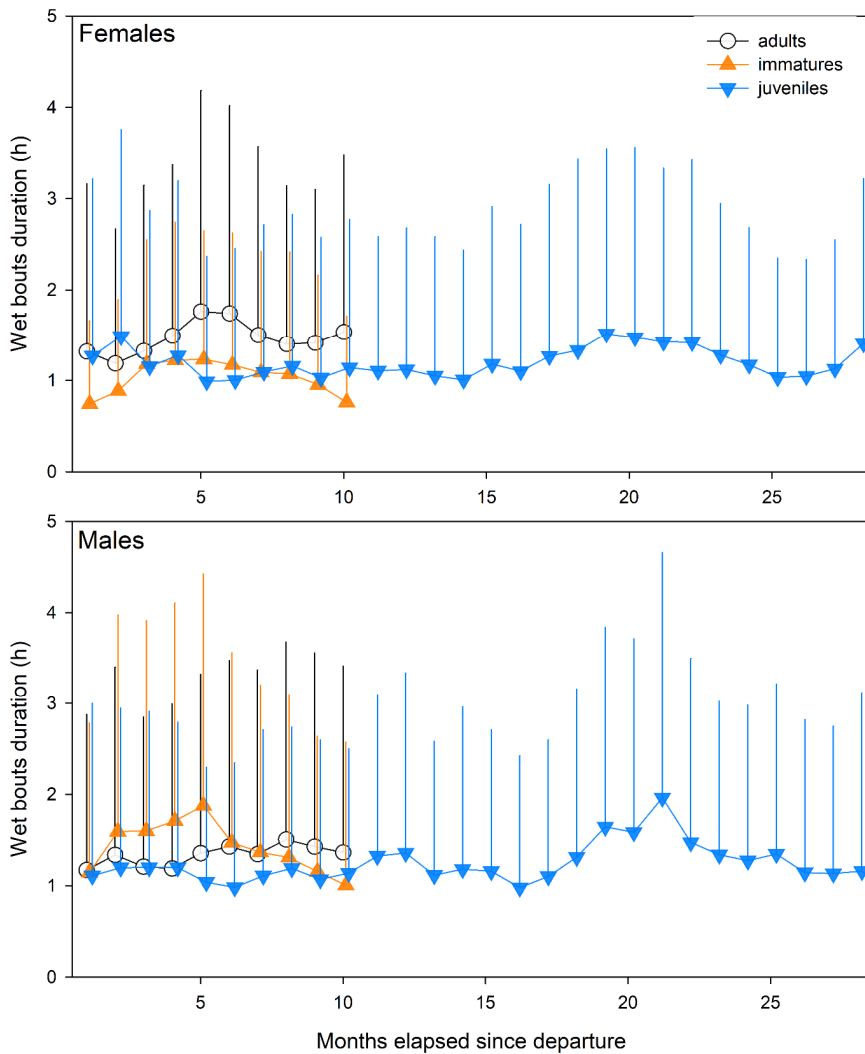
1553

1554 Figure S9 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles,
 1555 immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

1556

1557

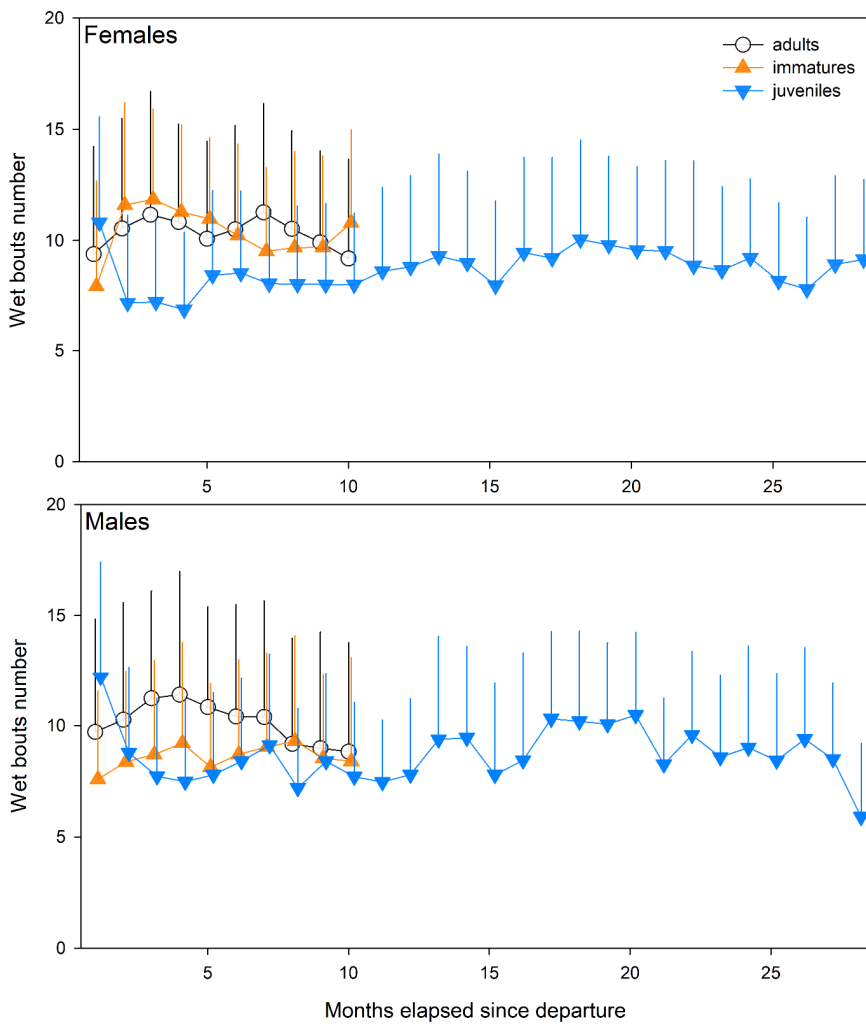
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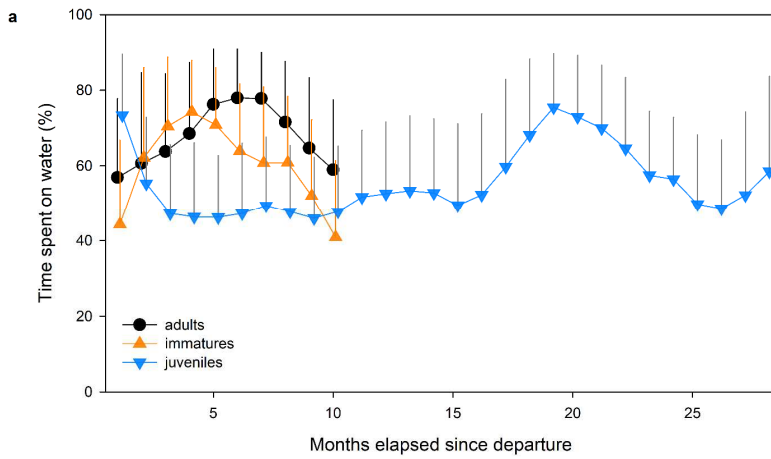
1560 Figure S10 Daily wet bouts duration (bouts on water in hours) for every month since departure of the
 1561 colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars
 1562 represent ± 1 sd

1563

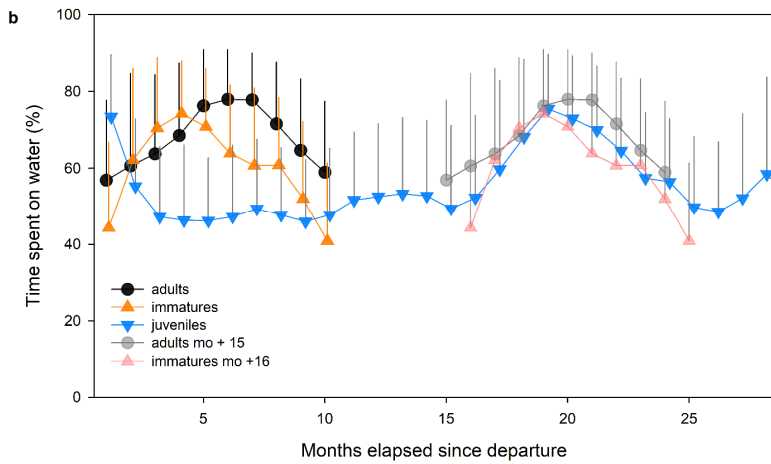


1564

1565 Figure S11 Daily wet bouts number (bouts on water) for every month since departure of the colony for
 1566 juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent
 1567 ± 1 sd
 1568



1569



1570

1571 Figure S12 Daily proportions of time spent on water for every month since departure of the colony for
 1572 juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel)
 1573 and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error
 1574 bars represent ± 1 sd
 1575

1576

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1619

1620 **TITLE**

1621 **The challenges of independence: ontogeny of at-sea behaviour in a long-lived**

1622 **seabird**

1623

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1628

1629 **Abstract**

1630 The transition to independent foraging represents an important developmental stage in the life cycle of
1631 most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less
1632 well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher
1633 mortality including that of inadequate/inferior foraging skills compared to adults, young naïve individuals
1634 combining lack of experience and physical immaturity. Thus a change in behaviour, resulting in an
1635 improvement of skills acquired from growing experience, is expected to occur during a period of learning
1636 through the immaturity phase. Very few studies have investigated the ontogeny of foraging behaviour
1637 over long periods of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining
1638 individual tracking data over several years. We investigated the foraging behaviour, through activity
1639 patterns, during the ~~successive-three~~ life stages of the endangered Amsterdam albatross by using
1640 miniaturized activity loggers on naïve juveniles, immatures and adults. ~~Naïve juveniles; naïve birds~~ during
1641 their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of
1642 time spent sitting on water, ~~higher-duration~~longer and more numerous bouts on water, ~~and lower~~
1643 ~~duration~~shorter and ~~less numerous~~fewer flying bouts). Patterns of activity parameters in juveniles after
1644 independence suggested a progressive change of foraging performances during the first two months since
1645 fledging. Juveniles reached similar activity values to those of immatures and adults as early as the 2nd-3rd
1646 months since independence, suggesting a progressive improvement of foraging performances during the
1647 first two months since fledging. We found sex differences support for the body-size hypothesis with
1648 respect to sex differences in activity parameters according to time ~~elapsed~~ since departure from the
1649 colony and month of the year, consistent with the important sexual dimorphism in the Amsterdam
1650 albatross. ~~Whatever th~~Regardless eof life stage considered, activity parameters exhibited temporal
1651 variability reflecting the modulation of foraging behaviour. This variability is discussed possibly in light

1652 ~~of~~linked to both extrinsic (i.e. environmental conditions such as variability in food resources or in wind)

1653 and intrinsic (i.e. energetic demands linked to plumage renew during moult) factors].

1654

1655

1656 **Keywords:** activity data loggers; foraging behaviour; southern Indian Ocean; Amsterdam albatross;

1657 *Diomedea amsterdamensis*

1658

1659 **Introduction**

1660 The transition from parental food dependency to independent foraging represents an important
1661 developmental stage in the life cycle of most vertebrate animals (Mushinsky et al. 1982; Margrath and Lill
1662 1985; Martin and Bateson 1985; Marchetti and Price 1989; Langen 1996; Burns et al. 2004) and is
1663 increasingly documented in a wide range of taxa (reptiles, birds, and some mammals). ~~Juveniles differ
1664 from adults in various life history traits and tend to survive less well than adults in most long-lived animals
1665 (Ydenberg 1989; Menu et al. 2005; Oppel et al. 2015; Cheng et al. 2019). Several hypotheses have been
1666 proposed to explain higher mortality observed for young individuals compared to adults (Healy et al.
1667 2019). One of the most widely accepted hypotheses is inadequate/inferior foraging skills of juveniles
1668 compared to adults, young naïve individuals combining lack of experience and physical immaturity (Lack
1669 1954; Daunt et al. 2007). Thus, a change in behaviour, resulting ~~in~~ from an improvement of skills acquired
1670 from increasing experience is expected to occur during a period of learning through the immaturity phase.
1671 ~~Learning often refers to stimulus-response associative learning ('trial and error'; Ruaux et al. 2020),
1672 although other forms of learning (such as social learning or imprinting) are also taken into account when
1673 considering the ontogeny of complex behaviours (Heys 1994; Wynn et al. 2020). Such a learning process
1674 has been studied on various taxa from insects to primates (Bruner 1972; Caubet et al. 1992; Dukas 2006;
1675 Rapaport and Brown 2008). Learning often refers to stimulus response associative learning ('trial and
1676 error'; (Ruaux et al. 2020)), although other forms of learning (such as social learning or imprinting) are
1677 also taken into account when considering the ontogeny of complex behaviour (Heys 1994; Wynn et al.
1678 2020).~~
1679 Juvenile birds are known to undertake vagrant erratic journeys during the post-fledging period especially
1680 in passerines (Naef-Daenzer and Gruebler 2008; Becker 2014; Evans 2018; Boynton et al. 2020), in raptors
1681 (Urios et al. 2010; Krüger et al. 2014; Harel et al. 2016) and in seabirds (Riotte-Lambert and Weimerskirch
1682 2013; Collet et al. 2020). Recent studies highlighted that the flight capacities and foraging behaviour of~~

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Mis en forme : Anglais (Royaume-Uni)

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1683 juveniles differed from those of adults in storks (Rotics et al. 2016), raptors (Harel et al. 2016; Nourani et
1684 al. 2020) or seabirds (Ydenberg 1989; Péron and Grémillet 2013; de Grissac et al. 2017; Corbeau et al.
1685 2020). Most flight components were found to improve over time to tend towards those of adults (Riotte-
1686 Lambert and Weimerskirch 2013; de Grissac et al. 2017; Corbeau et al. 2020).

1687 However, studies focusing on the foraging behaviour of juveniles remain scarce because of the difficulty
1688 to obtain individual tracking data for long periods, especially for long-lived pelagic seabirds with deferred
1689 maturity. Moreover, existing studies comparing flight capacities and foraging behaviour between juveniles
1690 and adults in such species only collected data during the first few months that juveniles spent at sea. Since
1691 juveniles may spend several years at sea before returning to a colony to breed, our understanding of the
1692 ontogeny of flight capacities and foraging behaviour remains fragmentary.

1693 The Amsterdam albatross *Diomedea amsterdamensis* is a large and long-lived pelagic seabird with an
1694 extended immaturity stage (~ 9 years Rivalan et al. (2010)). Similarly to a closely related species, the
1695 wandering albatross *D. exulans*, their foraging strategy relies on very low flight costs as a result of their
1696 dynamic soaring flight, whereby individuals optimize the orientation of their movement with wind
1697 direction to maximize the daily distance covered (Pennycuik 1982). During initial post-fledging dispersal
1698 juveniles disperse-wander alone over very long distances from their colony. At sea distribution during
1699 every stage of the life-cycle of Amsterdam albatross was studied by Thiebot et al. (2014) and de Grissac
1700 et al. (2016) who compared flight trajectories (i.e. departure direction or orientation toward specific
1701 areas) ~~movement patterns~~ of juveniles and adults, ~~namely trajectories (i.e. departure direction or~~
1702 ~~orientation toward specific areas)~~. Both studies concluded on slight differences among stages in
1703 distribution due to the extensive area they used. However, foraging behaviour is known to be constrained
1704 by intrinsic factors such as sex, age, reproductive status and body size across a wide range of taxa and
1705 hence play a key role in shaping activity (King 1974; Alerstam and Lindström 1990; Wearmouth and Sims
1706 2008). To understand the ~~potentially~~ changes in foraging proficiency according to experience (life-history

1707 stages), longitudinal studies of individuals spanning critical periods of their lives are thus required.
1708 Advances in animal-borne instrumentation enable key component of foraging behaviour such as foraging
1709 effort and activity to be recorded over long periods.

1710 In this study, we benefited from a unique dataset of different life stages (juveniles, immatures and adults)
1711 and a remarkable duration (up to 28 months for juveniles) to characterise and compare the behaviour
1712 changes when birds leave the colony for several months (immatures and adults) or years (juveniles). ~~✱~~
1713 ~~this study.~~ ~~Here, we~~ ~~compare~~ ~~analyse~~ the foraging behaviour, through activity patterns, of naïve
1714 juveniles (first years of independence at sea), immatures (individuals that never bred, age 2-10 years) and
1715 adults (individuals that bred at least once, age 8-28 years) of Amsterdam albatross (Table 1). By using
1716 miniaturized activity loggers (Global Location Sensing; GLS) to infer foraging behaviour (activity)
1717 throughout the successive life stages we addressed the following questions: i) do individuals belonging to
1718 different life-stages behaved differently? ii) are there differences in activity patterns between life-stages,
1719 ~~namely time spent on water and flying bouts~~, and are there detectable progressive changes? However,
1720 the loggers used does not yet allow to have longitudinal data and to cover the entire period until an
1721 individual is recruited into the population as a breeding adult, i.e. at least 8 years.

1722 Previous knowledge of the ecology of large albatrosses and Amsterdam albatross described above
1723 provides a practical framework for testing predictions about variability in foraging behaviour associated
1724 with ~~sex~~, stage, time elapsed since departure from the colony, ~~and~~ seasons and sex which are summarised
1725 in Table S1. Given the overlap of spatial distribution between life-stages (not presented here but see
1726 Thiebot et al. 2014; de Grissac et al. 2016; Pajot et al. 2021) we predicted that juveniles would compensate
1727 for any lack of foraging proficiency by increasing foraging effort and time (i.e. lower time spent on water
1728 and longer flying bouts, in other words decreasing time sitting on water and longer and more numerous
1729 bouts in flight; Hypothesis (BA), Table S12). We also predicted ~~sharp~~ changes in activity following fledging
1730 of juveniles from the colony followed by more progressive changes. Based on results found on fledglings

1731 wandering albatross (Riotte-Lambert and Weimerskirch 2013; Pajot et al. 2021) showing that juveniles
1732 reached some adult foraging capacities in less than two months, we predicted that ~~important~~ changes
1733 should be detected in activity parameters early after the juvenile left the colony (within few first months).

1734 Overall, juveniles should show ~~higher-contrasted~~ foraging effort (i.e. longer time spent on water, shorter
1735 flying effort with fewer and shorter flying bouts) just after fledging compared to other life-stages (~~i.e.~~
1736 ~~lower time spent on water, longer flying bouts and shorter water bouts~~). Due to seasonal changes in food
1737 availability individuals will face at sea after leaving the colony and the alleviation of energetic constraints
1738 linked to reproduction (for breeding adults) or to alternate foraging trips at sea and period on land for
1739 pair bonding and mating display (for immature birds), we predicted that adjustments of activity will occur
1740 according to the time spent (i.e. in months elapsed) since the departure of individuals from the colony
1741 (Hypothesis ~~(EB)~~, Table 2S1). In juveniles, we predicted early and rapid changes after fledging and then
1742 more progressive changes. Due to environmental changes occurring throughout the seasons we predicted
1743 temporal (i.e. related to the month of the year) changes in activity parameters for all life-stages
1744 (Hypothesis ~~(DC)~~, Table 2S1). Although food availability may be lower during winter, foraging effort may
1745 also be reduced when adults and immatures are moulting (Weimerskirch 1991). Moult is an intrinsically
1746 costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen
1747 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and
1748 thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized albatrosses like
1749 Amsterdam albatross, replacement of primary feathers lasts for more than one breeding season, and the
1750 moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch 1991). Partial
1751 moulting is suspected to occur outside the breeding period and to result in reduced activity (i.e. more
1752 time spent on the water; Weimerskirch et al. 2015, 2020). We therefore predicted a period of reduced
1753 activity that differs according to the life-stages and may be confounded by seasonal variability (Hypothesis
1754 (C). Lastly, due to sex differences in flight performances (Shaffer et al. 2001; Clay et al. 2020), specifically,

1755 due to their higher wing loading, males should both maintain longer flying effort, and be more likely to
1756 minimize the number of flying bouts than females. Thereupon, and based on results on wandering
1757 albatross (Riotte-Lambert and Weimerskirch 2013), similar pattern should be maintained outside the
1758 breeding period. We thus predicted differences in foraging behaviour between sexes (i.e. time spent on
1759 water, duration and number of flying and water bouts; Hypothesis (A_D), Table 2S1).

1760

1761 **Materials and methods**

1762 **Study species and data loggers**

1763 Amsterdam Island (37° 50' S; 77° 33' E) is located in the subtropical part of the southern Indian Ocean.

1764 In this oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder
1765 sub-Antarctic waters (Belkin & Gordon 1996). Though the diet and foraging strategy of Amsterdam
1766 albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that
1767 of the wandering albatross, although subtle differences can appear (Pajot et al. 2021; see Supplementary).
1768 Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large
1769 squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The
1770 wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction
1771 during the day (Nevitt et al. 2008). This strategy referred as 'foraging-in-flight' is the lowest energy
1772 consuming feeding strategy for the wandering albatross (Weimerskirch et al. 1997b). However, this
1773 strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014), leading to
1774 a more important utilization of the 'sit-and-wait' technique and possibly to vary depending on sites
1775 suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques
1776 could result in more frequent and shorter bouts on the water in the former technique (compared to
1777 'foraging-in-flight').

1778 The Amsterdam albatross, like other great albatrosses, is a biennial breeder (Roux et al. 1983; Jouventin
1779 et al. 1989), with high survival during juvenile, immature and adult phase (Rivalan et al. 2010). The adults
1780 that raised a chick successfully do not start a new breeding cycle after chick fledging, but remain at sea
1781 for a sabbatical period (~1 yr; Table 1; Rivalan et al. 2010). However, early failed breeders may start to
1782 breed the following year (Rivalan et al. 2010). Immature birds may visit the colony when they are 4–7 yrs
1783 old, but generally only start breeding at 9 yrs old (Table 1; Weimerskirch et al. 1997a). Juvenile birds
1784 fledge and migrate independently from the adults in January (Table 1). Exact fledging dates were not
1785 known for juveniles but were assessed from activity pattern as juvenile birds land on water quickly after
1786 leaving the colony (Weimerskirch et al. 2006). Amsterdam albatrosses were monitored annually since
1787 1983 and all individuals were individually marked (numbered stainless steel and plastic engraved colour
1788 bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age (79 individuals since the
1789 beginning of the study) and chicks of the year were banded, weighed (body mass \pm 50 g using a Pesola®
1790 spring balance) and measured (wing length \pm 1 mm with a ruler, tarsus length, bill length, and bill depth \pm
1791 0.1 mm with calipers).

1792 Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical
1793 period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale ~~dispersal-migratory~~
1794 ~~movements~~ (*sensu* Weimerskirch et al. 2015a) reaching >4000 km from the colony exploiting continuously
1795 warm waters (~18°C). No clear longitudinal seasonality existed in the movements of adults, nonetheless
1796 they tended to move westwards in June/July and eastwards in November. The immature birds moved
1797 widely in longitude (0° to 135° E), exploiting exclusively warm waters 17°-18° C. Similarly to adults no clear
1798 longitudinal seasonality synchronicity existed in the movements, except that they also tended to move
1799 westwards in June and eastwards in November. Juveniles exhibited very large ~~dispersal-migratory~~
1800 capacities over the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony),
1801 through a large range of latitudinal gradient (27° to 47° S). Juveniles birds tended to ~~disperse-migrate~~

1802 westwards first in March-April and temporarily exhibited synchronous individual movements. De Grissac
1803 et al. (2016) compared trajectories (i.e. departure direction or orientation toward specific areas) of
1804 juveniles and adults and showed that juveniles performed an initial rapid movement taking all individuals
1805 away from the vicinity of their native colony, and in a second time performed large-scale movements
1806 similar to those of adults during the sabbatical period. High individual variability and no clear differences
1807 between juveniles and adults patterns were found, except that adults foraged at significantly higher
1808 latitudes. De Grissac et al. (2016) concluded in an overlap in distribution between adults and juveniles due
1809 to the extensive area they used and their differences in latitudinal distribution compared to other
1810 Procellariiformes species.

1811 ~~Global Location Sensing (GLS) are archival light-recording~~ loggers ~~were~~ used to study activity of birds over
1812 periods lasting up to ~ 2 years. GLSs record the ambient light level every 10 min, from which local sunrise
1813 and sunset hours can be inferred to estimate location every 12 h (Wilson et al. 1992). GLS also recorded
1814 saltwater immersion data. ~~Immersion loggers by tested testing~~ for saltwater immersion every 30 s, storing
1815 the number of samples wet (>0) at the end of each 10 min period. We used saltwater immersion to
1816 estimate daily activity budget. Despite the higher mean spatial error of location estimates with these
1817 devices (over 100 km; Phillips et al. (2004a)), GLS loggers allowed us to track the birds for prolonged
1818 periods with minimal disturbance to them. We considered the following stages regarding the year of GLS
1819 deployment (see Table 1): juvenile, as a fledgling equipped with a GLS just before leaving the colony for
1820 the first time; immature, as a non-breeding young bird that had never bred equipped with a GLS when
1821 visiting the colony; adult, as a breeding adult equipped with a GLS during the incubation or brooding
1822 period which successfully fledged a chick and thereafter took a sabbatical year. To date, we have retrieved
1823 40 of the 50 GLS loggers deployed in total over 4 years, from which 33 individual tracks were estimated
1824 (Table 2). Our original aim was to collect activity data over the three life-stages on a long period of time

1825 (>1 year). These data are available from a total of 10 adults tracked throughout their sabbatical period,
1826 13 immature birds and 10 juvenile birds (up to 3.2 years).

1827

1828 **Data processing**

1829 The raw immersion data were obtained from testing saltwater immersion every 30 s, the GLS storing the
1830 number of samples wet (> 0) at the end of each 10 min period. The data were values from 0 (no immersion
1831 or dry, in flight or sitting on the ground) to 200 (permanently immersed in sea water or wet), indicating
1832 the number of 3 s periods during 10 min blocks when the sensor was immersed in saltwater. Loggers
1833 recorded proportion of time in seawater at 10 min intervals, which we summarized as hours in the water
1834 per day (hereafter time spent on water~~PROWATER~~; 10 min blocks immersion data > 0). This measure is a
1835 reliable proxy of foraging effort linked to foraging behaviour of the species which enters the water
1836 principally to forage (Weimerskirch and Guionnet 2002). Additionally, the duration of the bouts spent
1837 entirely immersed (10 min blocks immersion data = 200) was calculated daily (hereafter referred as wet
1838 bouts duration~~WETBOUITS~~). Conversely, when birds are not on land, the time spent dry was interpreted
1839 as flying (and thus not feeding). The duration of the bouts spent entirely dry (10 min blocks immersion
1840 data = 0) was calculated daily (hereafter referred as dry bouts duration~~DRYBOUITS~~). Additionally the
1841 numbers of bouts (number of wet bouts ~~-sitting on water-on-water-~~ ~~WETBOUITSNB~~ and of dry bouts ~~-~~
1842 ~~flying-~~ ~~DRYBOUITSNB~~) were obtained daily. Although the loggers integrated activity within each 10 min
1843 block and so did not provide the exact timing of landings and take-offs, Phalan et al. (2007) found for
1844 comparative purposes that bouts defined as a continuous sequence of 0 values for flight (dry) and a
1845 sequence of values of 1 or greater for wet bouts, were suitable proxies for activity.

1846 To select the data corresponding to periods spent at sea after leaving the breeding site, we used the
1847 following criteria on activity to define the departure time from the colony for each stage: 1) juveniles, the
1848 first bout spent on seawater (wet bouts duration~~WETBOUITS~~) > 1h based on PTT tracking data

1849 (Weimerskirch et al. unpublished data); 2) immatures and adults, the last bout spent flying (dry bouts
1850 durationDRYBOOTS) > 12h based on PTT tracking data (Weimerskirch et al. unpublished data). Using these
1851 criteria we obtained departure months as follows: 1) the juveniles fledged from the colony from January
1852 to March, 2) the immatures left between April and August, and 3) the departures of sabbatical adults were
1853 spread over two periods, first between December and February and then from May to July.

1854

1855 **Statistical analyses**

1856 ~~Differences between sexes in body measurements were tested using Student's t tests and Wilcoxon~~
1857 ~~rank tests (see Supplementary A).~~

1858

1859 Variation in activity parameters

1860 The aim was to determine whether distinct foraging behaviours could be detected across the
1861 patterns of variation of wet/dry data dynamics, and then to appraise how use of these
1862 behaviours varied over time and among individuals. First, to deal with the fact that wet/dry
1863 metrics some explanatory variables were interrelated might covary (number of wet bouts sitting on water
1864 and time spent on water, wet bouts duration and dry bouts duration, wet bouts number and dry bouts
1865 number) and to avoid unnecessary redundancy, we ran principal components analyses (PCA built with the
1866 'PCA' function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe
1867 behaviours using gradients of activity we ran PCA for i) all stages (PCS; based on activity data collected
1868 during the first ten months post-departure) and for ii) juveniles only, as an additional goal was to
1869 determine changes in activity patterns during the first two years of life (PCJ; based on activity data
1870 collected during the first twenty-nine months post-departure).
1871 Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance.
1872 The first principal component (PC1S) explained 41.5% of the total variance, and correlated positively with

1873 time spent on water (r = 0.97) and negatively with dry bouts number (r = -0.79). The second principal
1874 component (PC2S) explained 32.5% of the variation and correlated positively with wet bouts duration (r
1875 = 0.79) and negatively with wet bouts number (r = -0.75). The third principal component (PC3S) explained
1876 20.2% of the variation and correlated positively with dry bouts duration (r = 0.74) and negatively with dry
1877 bouts number (r = -0.44).

1878 Considering juveniles, the first three principal component (PCJ) explained 92.2% of the total variance. The
1879 first principal component (PC1J) explained 42.3% of the total variance, and correlated positively with time
1880 spent on water (r = 0.98) and negatively with dry bouts number (r = -0.76). The second principal
1881 component (PC2J) explained 32.2% of the variation and correlated positively with wet bouts duration (r =
1882 0.72) and negatively with wet bouts number (r = -0.75). The third principal component (PC3J) explained
1883 20.7% of the variation and correlated positively with dry bouts duration (r = 0.48) and negatively with dry
1884 bouts number (r = -0.46) and wet bouts duration (r = -0.46).

1885
1886 Second, we then used generalized additive mixed-additive models (GAMMs, built with the 'gam'
1887 function, itsadug and mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with
1888 each of the three first axes of the PCA principal components analyses as the dependent variable. We
1889 separately ran models testing for variability in activity parameters i) for all stages combined (PCS) and ii)
1890 for juveniles (PCJ), based on different duration of datasets (28 months since departure for juveniles and 9
1891 months since departure for immatures and adults; see Supplementary; Table S2). Thus, for all stages
1892 combined i) we considered the lowest number of months elapsed since departure available (9 months
1893 since departure). To investigate the causes of variability of the activity parameters during 24h (sitting on
1894 water — time spent on waterPROPWATER, wet bouts durationWETBOUITS and dry bouts
1895 durationDRYBOUITS duration, WETBOUITSNB wet bouts number and dry bouts numberDRYBOUITSNB
1896 numbers) we used generalized linear mixed effects model. Months elapsed since departure (the duration

1897 elapsed since fledging expressed in month, i.e. the first month after fledging and so on), month of the year
1898 (i.e. January and so on), sex, and stage (only for i) were included as fixed effects, ~~and random slopes and~~
1899 ~~intercept to allow activity parameters to randomly vary between individual and time elapsed since~~
1900 ~~departure (Zuur 2009a). We also added the use of #1~~To test for the importance of individual variability in
1901 our results we built models with or without random effects ~~individual identity as a random effect permit~~
1902 ~~to account for pseudo-replication issues, since the same individual provided several values. We compared~~
1903 ~~models without random effect, models with random intercepts, and models with random slopes and~~
1904 ~~intercepts to test whether the rate of change of activity parameters as a function of time elapsed since~~
1905 ~~departure varied between individuals (Zuur 2009a). Models included month elapsed since departure as a~~
1906 ~~continuous covariate~~fixed factors modelled with non-parametric smoothing functions (Wood 2017). We
1907 limited the amount of smoothing (k) with the 'gam.check' function following Wood (2017) for each spline
1908 to avoid excessive flexibility and model overfitting that would have no ecological meaning. Month elapsed
1909 since departure and month of the year were used to test for time variation in activity parameters. We
1910 considered the number of months elapsed since departure available for all individuals (28 months since
1911 departure for juveniles and 9 months since departure for immatures and adults). ~~Thus, for all stages~~
1912 ~~combined we considered the lowest number of months elapsed since departure available (9 months since~~
1913 ~~departure). We first ran models testing for variability in PROPWATER, WETBOUITS, DRYBOUITS,~~
1914 ~~WETBOITSNB and DRYBOITSNB independently for each stage (juvenile, immature and adult) and then~~
1915 ~~by combining all stages (see Supplementary B; Table S2).~~
1916 Models investigating the causes of variability of PROPWATER (GLMM 1 to 4, Table S2) were fitted using
1917 the package MASS and nlme and the function "lme" (Zuur 2009; Pinheiro et al. 2013). Response variables
1918 were visually tested for normality (through Q-Q plots) and homoscedasticity (using Cleveland dotplots;
1919 (Zuur et al. 2010) before each statistical test. The error structure approached the normal distribution, and
1920 therefore a Gaussian family (link = "identity") was selected for all models.

1921 Models investigating the causes of variability of WETBOUITSNB and DRYBOUITSNB (GLMM 9 to 16, Table
1922 S2) were fitted using the MASS, lme4 packages and the function “glmer” (Zuur 2009; Pinheiro et al. 2013;
1923 Bates et al. 2014) with a Poisson distribution. Models validation was done following Zuur et al. (2009).
1924 Models for PROPWATER, WETBOUITSNB and DRYBOUITSNB including all combinations of explanatory
1925 variables and random effects were then tested and ranked using their Akaike Information Criterion (AIC)
1926 values and Akaike weights following the Information-Theoretic Approach (Burnham and Anderson 2002).
1927 The model with the lowest AIC was considered as the best model. Two models separated by a difference
1928 in AIC values of less than 2 were assumed to fit the data similarly.

1929 Models investigating the causes of variability of WETBOUITS and DRYBOUITS (glmmPQL 1 to 8, Table S2)
1930 were fitted using the function “fitdist” from the package DHARMA to assess the fit of residuals to a Gamma
1931 distribution. In this case, we fitted final models with penalized quasi likelihood using the glmmPQL
1932 function in the package MASS (Venables and Ripley 2002). This meant that model simplification could
1933 proceed only on the basis of marginal Wald t tests produced in the model summary ((Bolker et al.
1934 2009) Table S7a). We therefore refitted models without interactions (i.e. sex * month.elapsed for models
1935 for juveniles), until all remaining terms were significant ((Crawley 2012) for models specifications and
1936 sample sizes see Supplementary material Appendix 1, Table S7b).

1937 Multi-collinearity among covariates was assessed using variance inflation factors (GVIFs, AEDForecasting
1938 library in R (Zuur 2009)) and a cut-off value of 3 was used to remove collinear variables prior to modeling.

1939

1940 Variation in body size with sex

1941 Differences between sexes in body size measurements were tested using Student’s t-tests and Wilcoxon
1942 rank tests (see Supplementary A). We tested independently if each body-measurements (wing length,
1943 tarsus length, bill length, bill depth and body mass) varied according to sex and stage (juvenile and adult).
1944 The effects were tested using generalised linear models (GLMs) with a Gaussian family and identity link

1945 function (Zuur 2009b). Model validation and model selection were performed following (Zuur 2009b).
1946 Although sexes and stages differed for some body size measurements, we could not include body size as
1947 an additional explanatory variable in GAMMs testing for factors of variation in activity patterns due to
1948 small sample sizes in each sex and stage category, and due to unbalanced sampling.

1949 Spatial and statistical analyses were performed using (R Core Team 2021). Values are means \pm SD.

1950

1951 **Results**

1952

1953 Changes in activity parameters for all between stages

1954 The most parsimonious models (i.e. lowest AICc) explaining variations in activity parameters in
1955 Amsterdam albatross included time (time elapsed since departure from the colony, and month of the
1956 year), stages and sexes (Table 3; Supplementary Figures S1 - S5; Tables S2 and S3), whatever the synthetic
1957 activity variables considered (PC1S, PC2S and PC3S). Selected models also included random
1958 effects on intercepts and slopes, indicating inter-individual variability in activity and inter-individual
1959 variability in the rate of change of activity as a function of time elapsed since departure from the colony.

1960 The three synthetic activity covariates (PC1S, PC2S, PC3S) varied significantly with stage and
1961 sex (Supplementary Figures S1 - S5; Tables S2 and S3). Compared to adults, immatures and even more so

1962 juveniles, tended to spent a lower percentage of time on water (Table 4, Supplementary Figures S1) and
1963 to make more flying bouts (PC1S; Supplementary Figures S2), made shorter and fewer bouts on water

1964 (PC2S; Supplementary Figures S4-S5), and made longer flying bouts (PC3S; Supplementary Figures S2).

1965 Males tended to spent a higher percentage of time on water and to make fewer flying bouts (PC1S),
1966 longer and more numerous bouts on water (PC2S) and shorter flying bouts (PC3S) compared to females.

1967 The two synthetic activity variables covariates (PC1S, PC2S) also varied significantly with time exhibiting
1968 clear nonlinear temporal patterns (Figure 1). These variations were related to the time elapsed since their

1969 ~~departure from the colony and showed seasonal changes (indicated by the month of the year;~~
1970 ~~Supplementary Figures S1 - S5; Tables S2 and S3). With increasing time since departure~~ The birds tended
1971 ~~to spend lower percentage of time on water and made shorter wet bouts, but made longer dry bouts.~~
1972 ~~They spent less percentage of time on water make more flying bouts during the period March to July~~
1973 ~~compared to rest of the year (PC1S, Supplementary Figures S1 - S5). They made. The seasonal change is~~
1974 ~~also observed through longer and fewer bouts spent on water during the period April to November, and~~
1975 ~~shorter flying bouts during the period SeptemberNovember to DecemberFebruary at the end of the year~~
1976 ~~(PC2S: September-December; PC3S: October-December). Finally, juveniles showed strong and abrupt~~
1977 ~~temporal changes in activity linked to the time elapsed since departure from the colony, in other words~~
1978 ~~their behaviour changed~~ in the first two months after fledging (Supplementary Figure S6). In immatures
1979 ~~and in adults the temporal pattern appeared reversed compared to juveniles (Supplementary Figure S6).~~
1980
1981 *Changes in aActivity of parameters in juveniles duringin the first two years after fledging*
1982 In juveniles Amsterdam albatross, the most parsimonious models explaining variations in activity
1983 ~~parameters included time (time elapsed since departure from the colony, and month of the year)~~
1984 ~~whatever the activity variablesgradients considered (Table 5; PC1J, PC2J and PC3J), and sexes (PC2J and~~
1985 ~~PC3J). Selected models also included random effects on intercepts and slopes, indicating inter-individual~~
1986 ~~variability in activity and inter-individual variability in the rate of change of activity as a function of time~~
1987 ~~elapsed since departure from the colony (STable XSupplementary Figures S7).~~
1988 ~~The second and third covariates (PC2J and PC3J) varied significantly with sex (Supplementary Figures S8 -~~
1989 ~~S11; Tables S5b, 5c), indicating that juvenile males tended to make shorter and more numerous bouts~~
1990 ~~on water (PC2J) and shorter flying bouts (PC3J) compared to females (Supplementary Figures S8 - S11;~~
1991 ~~Tables S5b, 5c). The first two activity covariates (PC1J and PC2J) also varied significantly with time~~
1992 ~~exhibiting clear nonlinear temporal patterns (Figure 2). These variations were related to the time elapsed~~

1993 ~~since their departure from the colony and showed seasonal changes (indicated by the month of the year;~~
1994 ~~Supplementary Figures S8 - S12; Tables S2 and S4a, 4b). Juveniles~~The birds seemed to alternate periods
1995 ~~of lower percentage of time spent on water combined with more numerous flying bouts (April) with~~
1996 ~~periods of higher percentage of time on water combined with fewer flying bouts (February, July-October;~~
1997 ~~PC1J5, not illustrated). The seasonal change was also observed through longer and fewer bouts spent on~~
1998 ~~water and shorter flying bouts at the end of the year (PC2J5: September-December). Finally, juveniles~~
1999 ~~showed temporal changes in their behaviour linked to the time elapsed since departure from the colony~~
2000 ~~(Figure 2). In other words, during the first 28 months after fledging, they tended to increased the time~~
2001 ~~spent on water while decreasing the number of flying bouts (Figure 2a). The ship PC2J since departure~~
2002 ~~was indicating wet-bout duration~~
2003 ~~Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and~~
2004 ~~bill depth whatever the stage (juvenile or adult; see Supplementary A Table S2-S7). In juveniles, males~~
2005 ~~were ~13% heavier than females, while the difference was not significant in adults. The most sexually~~
2006 ~~dimorphic phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they~~
2007 ~~were body mass, tarsus length and bill length.~~
2008 ~~All stages exhibited clear temporal patterns in their activities, related to the time elapsed since their~~
2009 ~~departure from the colony and showing seasonal changes (indicated by the month of the year) whatever~~
2010 ~~the five activity metrics considered (Figures 1-5; Supplementary B Tables S2-S7d). Juveniles showed~~
2011 ~~strong temporal changes linked to the time elapsed since departure from the colony (Figure 1). From the~~
2012 ~~first month since departure, there was a quick decrease in the proportion of time spent on sea surface~~
2013 ~~(mean value for the 1st-month: 73.4±16.1%, for the 3rd-month: 47.2±18.3%), in the duration of bouts on~~
2014 ~~water (mean duration for the 1st-month: 1.21±1.93h, for the 6th-month: 0.99±1.42h) and in the numbers~~
2015 ~~of bouts on water (mean number for the 1st-month: 11.34±4.96, for the 3rd-month: 7.43±3.59), but an~~
2016 ~~increase in the duration of bouts flying (mean duration for the 1st-month: 0.89±0.97h, for the 3rd-month:~~

2017 1.38±1.45h), and the numbers of bouts flying (mean number for the 1st month: 6.18±3.14, for the 3rd
2018 month: 7.86±3.11). Although less pronounced, the activity (proportion of time spent on seawater, the
2019 duration of bouts on water and the numbers of bouts on water or flying; Supplementary B Tables S2) also
2020 varied according to the month of the year with two distinct periods (from November to February-March
2021 and from April-May to October). Highest values in the proportion of time spent on seawater, duration of
2022 bouts on water and numbers of bouts flying tended to be observed from November to February-March
2023 (Figure 1; Supplementary B Table S3a). In immatures and in adults the temporal pattern, i.e. months since
2024 their departure from the colony, of the activity parameters appeared generally reversed compared to
2025 juveniles (Figures 1-5; Supplementary B Tables S2, S3a-d, S4a-d, S5a-d, S6a-d, S7a-d). For the proportion
2026 of time spent on sea surface, the duration and the number of bouts on water, values were low early after
2027 departure then increased during the following months to peak ~ 3-5 months later, and finally tended to
2028 decrease at the end of the period. The opposite pattern was observed for duration and number of bouts
2029 flying. Regarding the seasonal changes (i.e. months of the year; Figures 1-5; Supplementary B Tables S2,
2030 S3a-S7d), for immatures, the temporal pattern tended to differ for all activity parameters when compared
2031 to that of months elapsed since departure. This was not the case for adults which exhibited alike temporal
2032 patterns. Furthermore, temporal patterns varied differently by sex whatever the stage considered (Figures
2033 2-5; Table 3).

2034
2035 When taking into account all three stages (juveniles, immatures and adults), interactions between the
2036 variables months elapsed since departure and stage, and between month of the year and stage were
2037 highly significant when explaining all the parameters of activity (proportion of time spent on seawater,
2038 the duration of bouts on water or flying and the numbers of bouts on water or flying; Supplementary B
2039 Tables S2). Therefore the difference between on one hand juveniles, and on the other hand immatures
2040 and adults depended on the number of months spent at sea since departure from the colony but also on

2041 the month of the year (Figures 1-5). Juveniles had very contrasted temporal patterns for all the activity
2042 parameters and almost never reached values of activity parameters observed for immatures and adults
2043 (Tables 4, Supplementary B Tables S3d, S4d, S5d, S6d, S7d, Figures S1-S4). This was all the more
2044 pronounced when considering the time spent on sea surface (Figure 1), the duration (Figure 4) or the
2045 numbers of bouts on water (Figure 5), and the numbers of flying bouts (Figure 3). Juveniles spent more
2046 time in flight, with more frequent bouts as early as the second to third months spent at sea after their
2047 departure. During the 9 first months spent at sea after departure all the activity parameters of juveniles
2048 differed in values and in patterns when compared to immatures or adults.

2049
2050 When comparing all three stages (juveniles, immatures and adults), interactions between the number of
2051 months elapsed and sex, and between month of the year and sex were highly significant when explaining
2052 almost all activity parameters (Appendix A Table S2).

2053
2054
2055 In juveniles during the first 28 months spent at sea (after departure) there was a significant effect of the
2056 time elapsed (months), the month of the year and the sex for all activity parameters considered except
2057 for the proportion of time spent on seawater (Table 3, Appendix A Tables S2, S3a, S4a, S5a, S6a, S7a,
2058 Figures 2-6). In juveniles, males tended to spend more time sitting on water (higher wet bouts duration)
2059 and more frequently (higher wet bouts numbers; Figures 4-5, Appendix A Figures S1-S4) than females.
2060 Nonetheless, these differences varied according to the time elapsed and with the month of the year. The
2061 time spent on the water by juveniles changed during the first 28 months at sea (Figure 6). While it
2062 decreased rapidly during the first two months after fledging, it remained low (47-52%) during the next 14
2063 months and then increased again. Interestingly, the same pattern as the one observed in immature and
2064 adult birds was found with a 15-16 months of delay in juveniles, reaching similar values (Figure 6).

2065 In immatures, males tended to spend more time sitting on water (higher time spent on water and wet
2066 bouts duration) but less frequently (lower wet bouts numbers; Table 3, Appendix A Tables S2, S3b, S4b,
2067 Figures 4–5) than females. Conversely, in juveniles and adults there was no significant effect of sex on the
2068 proportion of time spent on the water (Tables 4, Appendix A Table S2).

2069 In adults, males tended to spend less time flying (lower dry bouts duration) and flew less frequently (lower
2070 dry bouts numbers; Table 3, Appendix A Tables S4c, S5c, S6c, S7c; Figures 2–3) than females, but there
2071 was no significant effect of sex on the proportion of time spent on the water (Appendix A Tables S2, S3c).
2072 Depending on the activity parameters considered the difference between adult males and adult females
2073 appeared at different timing of the year (month of the year) and of their journey (months elapsed since
2074 departure; Figures 2–5, Appendix A Tables S4c, S5c, S6c, S7c). Occasionally these differences were more
2075 pronounced early after departure from the colony during the first four months (dry bouts duration; Figure
2076 2) or during the next few months (wet bouts duration figure 4 and dry bouts number Figure 3).

2077 *Body size*

2078 Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and
2079 bill depth whatever the stage (juvenile or adult; Tables 6–12). In juveniles, males were ~13% heavier than
2080 females, while the difference was not significant in adults (Table 6). The most sexually dimorphic
2081 phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they were body
2082 mass, tarsus length and bill length.

2083

2084 **Discussion**

2085 Using miniaturized activity loggers (GLS), we showed a clear differences and changes in activity
2086 characteristics depending on life-stages, time and/or sex. Elucidating the transition to independence in
2087 early life stages is crucial for understanding the causes of higher juvenile mortality in long-lived species
2088 (Fay et al. 2015; Payo Payo et al. 2016). By comparing changes in behaviour at sea and foraging

2089 parameters of juveniles ~~up to 28 months~~ after their departure at sea with those of immatures and adults
2090 in the Amsterdam albatross, we showed that juveniles differed from immatures and adults in their activity
2091 values and patterns. In this study, we benefited from a unique comprehensive dataset of remarkable
2092 duration (up to 28 months) to characterise the post-fledging behaviour of naïve seabirds. Although one
2093 limitation of our study was that individual longitudinal data were not long enough to explore changes in
2094 behaviour from fledging to the adult stage, these results provide new insights into the timing and the
2095 change of behaviour in naïve individuals over a unique dataset in a long-lived endangered seabird species.
2096 One of the limitations of our study is that no sufficient long individual longitudinal data exist to explore
2097 the change of behaviour from fledging to the adult stage.

2098

2099 Stage specific changes

2100 The birds were found to behave differently according to their stage whatever the activity
2101 variables ~~gradients~~ ~~covariates~~ considered, indicating differences in foraging behaviour. Overall, ~~Globally~~
2102 juveniles ~~tended to spend~~ lower percentage of time on water compared to immatures and adults.
2103 Nonetheless, ~~During~~ during the first month following their departure from the colony, ~~while juveniles~~ ~~the~~
2104 proportion of time spent on water by ~~the immatures and the adults~~ showed a ~~typical~~ dome-shaped curve
2105 peaking ~~with a maximum~~ three to five months after their departure, ~~the juveniles~~ ~~spent a greater~~ ~~changed~~
2106 abruptly ~~proportion of time sitting on water~~, with values dropping off in the first two months and then
2107 remaining low and overall lower than in adults and immatures ~~did longer and more numerous bouts on~~
2108 water, and ~~shorter and less numerous flying bouts than immatures and adults~~. This might indicate a lower
2109 foraging activity ~~effort~~ in naïve birds. During the same period, the ~~gradient~~ duration and ~~number of water~~
2110 bouts also exhibited ~~also~~ progressive change, ~~but nonlinear trend with the lowest duration reached by mi~~
2111 period. ~~However~~, from the second month following departure from the colony ~~these patterns~~ ~~suggested~~
2112 an early and gradual change in foraging behaviour ~~reversed and the~~ ~~and~~ ~~suggested~~ that juveniles

2113 progressively behaved similarly to immatures and adults (reaching similar values in activity
2114 covariates) activity patterns of juveniles became similar to that of immatures and adults. It is noteworthy
2115 that the multi-monthly bell-shaped pattern observed during the first 10 months after departure in
2116 immatures and adults appears to be mirrored in juveniles 15-16 months later (see Figure S12). ~~only 10 to~~
2117 ~~17 months after fledging depending on the activity parameter considered (see Figure 6).~~ Together, these
2118 results suggest a progressive ~~behavioural changes~~ improvement of in movements ~~performances~~ during
2119 the first two months ~~after~~ since fledging. ~~Juvenile naïve birds during their first month at sea after leaving~~
2120 ~~their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, higher~~
2121 ~~duration and more numerous bouts on water, and lower duration and less numerous flying bouts). They~~
2122 ~~reach values similar to those of immatures and adults 2 to 3 months after departure (except for the~~
2123 ~~number of dry/wet bouts for which it took longer), suggesting a progressive improvement of foraging~~
2124 ~~performances during the first two months since fledging. This suggests~~ seems to indicate that juvenile
2125 individuals ~~are therefore very likely to~~ may have ~~poorer weaker~~ foraging skills during their first two
2126 months ~~spent~~ at sea. Although behavioural changes can often equate to improved performance (e.g.
2127 (Campioni et al. 2020) this is not always the case. The emergence of juvenile birds as more 'adult like' in
2128 their foraging/flight behavioural patterns is not necessarily a sign of improvement.
2129 Characteristics of immatures and adults Results suggest that immatures may differ from both adults and
2130 juveniles in some aspects of their behaviour. While most of the activity parameters and the temporal
2131 patterns showed similarities with adults when considering the time elapsed since departure, they seemed
2132 rather comparable to juveniles when considering seasonal aspects (month of the year). Such inconsistency
2133 can be explained by several non-exclusive explanations: i) similar management of energy constraints than
2134 adults, ~~as post-breeding~~ as adults and immatures are less constrained in their central-place foraging
2135 strategies (Campioni et al. 2016), ii) comparable capacity to respond to local resource availability in their
2136 foraging behaviour than juveniles (Frankish et al. 2022), and iii) incomplete acquisition of more long-term

2137 ~~learning of complex movement strategies~~ (Thorup et al. 2003; Votier et al. 2011; Rotics et al. 2016).

2138 ~~Disentangling among these hypotheses~~ ~~ement can be achieved by combining higher resolution movement~~

2139 ~~data with longer longitudinal studies~~ ~~y covering all three life stages for same individuals.~~

2140 ~~Elucidating the transition to independence in early life stages is crucial for understanding the causes of~~

2141 ~~higher juvenile mortality in long lived species (Fay et al. 2015; Payo Payo et al. 2016).~~ Since all stages of

2142 the Amsterdam albatross forage in the same water masses (see Thiebot et al. 2014), differences in

2143 foraging behaviour were presumably not due to different oceanographic characteristics as observed in

2144 other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al. 2020b). These lower

2145 performances could be due to a combination of lack of experience of optimal behaviours, poor knowledge

2146 of the environment, use of distinct cues and/or physical immaturity (Shaffer et al. 2001; Frankish et al.

2147 2020a, 2022). It is likely that increasing exposure to diverse foraging situations allows juveniles to rapidly

2148 accumulate foraging experience and improve various aspects of foraging.

2149 ~~What might be designated as The~~ ~~'lower performance'~~ of juveniles ~~we~~ ~~found in our study~~ is consistent

2150 with studies on wandering albatrosses and Amsterdam albatrosses (Riotte-Lambert and Weimerskirch

2151 2013; de Grissac et al. 2017; Pajot et al. 2021) during the first weeks at sea. Fledging juvenile albatrosses

2152 ~~behaved differently and which found~~ that shortly after ~~fledging juvenile albatrosses~~ ~~they~~ employ similar

2153 foraging strategies as adults (Frankish et al. 2022). Additional skills (such as detection of prey at the

2154 surface, detection of other foraging seabirds, navigational skills...) need to be acquired during the

2155 immature period before the efficiency of these behaviors matches that of adults. This is also typical of

2156 other seabird taxa, which show progressive improvement in flight performance with the numbers of days

2157 since fledging (Yoda et al. 2004; Mendez et al. 2017; Collet et al. 2020; Corbeau et al. 2020; Frankish et al.

2158 2022). For example juvenile brown boobies *Anous stolidus* improved their flight abilities (Yoda et al. 2004)

2159 and juvenile European shags *Phalacrocorax aristotelis* compensate for poor foraging success by increasing

2160 their foraging time during first months after fledging (Daunt et al. 2007). In contrast, flight capability (flight

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2161 speed and sinuosity) comparable to that of adults allows juvenile white-chinned petrels *Procellaria*
2162 *aequinoctialis* to rapidly flew large distances from the colony (Frankish et al. 2020).

2163 Notwithstanding the progressive ~~improvement change~~ of movement ~~performances-behaviours~~ (foraging
2164 parameters estimated from activity parameters improved with time elapsed) quantified in juvenile
2165 Amsterdam albatrosses, it remains elusive whether this is a question of physical development and/or a
2166 matter of gaining experience. Elucidating the transition to independence in early life stages is crucial for
2167 understanding the causes of higher juvenile mortality in long-lived species (Fay et al. 2015; Payo-Payo et
2168 al. 2016).

2169
2170 ~~Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross~~
2171 ~~forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013;~~
2172 ~~Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by~~
2173 ~~differences in foraging habitats. We found support for the body size hypothesis to explain sex differences~~
2174 ~~in activity parameters (except for the time spent on water), consistent with the important sexual~~
2175 ~~dimorphism in the Amsterdam albatross. Males tended to spend more time sitting on water (wet bouts~~
2176 ~~duration) whatever the stage, and depending on stage more (for juveniles) or less (for immatures and~~
2177 ~~adults) frequently compared to females. Consistently, we found that males tended to fly for shorter~~
2178 ~~periods (dry bouts duration) compared to what females did and possibly less frequently (dry bouts~~
2179 ~~number) depending on time. Whatever the stage, there was no significant effect of sex on the proportion~~
2180 ~~of time spent on the water (except in immatures where males tended to spent more time sitting on water~~
2181 ~~compared to females).~~

2182 ~~Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to~~
2183 ~~have very similar foraging behaviour compared to that of the Wandering albatross, although subtle~~
2184 ~~differences can appear (Pajot et al. 2021). (Delord et al. 2013) Although Amsterdam albatross is 5-8%~~

2185 smaller and 25% lighter than wandering albatross, the two species have a very close anatomy and similar
2186 use of the wind. In the wandering albatross, due to sex differences in flight performance, specifically, due
2187 to their higher wing loading, males should both maintain longer flying effort and be more likely to
2188 minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). Hence, wandering
2189 albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the
2190 day (Nevitt et al. 2008). This strategy referred as '*foraging in flight*' is the lowest energy consuming
2191 feeding strategy for the wandering albatross (Weimerskirch et al. 1997b). However, this strategy tends to
2192 change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a more important
2193 utilization of the '*sit-and-wait*' technique and possibly to vary depending on sites suggesting considerable
2194 behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent
2195 and shorter bouts on the water in the former technique (compared to '*foraging in flight*'). In other word,
2196 males may have more of a '*sit-and-wait*' strategy while females have more of a '*foraging-in-flight*'
2197 strategy, although there is some behavioural plasticity particularly over time. Our prediction that foraging
2198 behaviour differs between sexes was fully supported (i.e. sex differences in bouts duration and number).
2199 Nevertheless, the similarity in time spent on the water suggests that the differences may be more subtle,
2200 showing some a trade-offs in duration and numbers between flying and water bouts. This trade-off should
2201 vary depending on stage as immature females tended to have shorter and more frequent bouts on the
2202 water. This implies that while probably feeding on similar water masses, the sexes might differ in type of
2203 prey targeted and/or used different foraging methods. The confirmation of this hypothesis reinforces the
2204 fact that the two sibling species, as previously assumed, show a high degree of similarity in their foraging
2205 behaviour.

2206 Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex
2207 usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can
2208 result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey

2209 ~~(Gonzales Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019;~~
2210 ~~Barbraud et al. 2019). It has also been suggested that size matters probably because the smaller and~~
2211 ~~lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower~~
2212 ~~wing loaded female wandering albatrosses, compared to males, are probably better able to exploit~~
2213 ~~subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that~~
2214 ~~females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than~~
2215 ~~males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al.~~
2216 ~~(2002); Stauss et al. (2012)).~~

2217

2218 Temporal changes in activity

2219 The temporal variability of activity was found whatever the life-stage considered. Part of the activity
2220 changes observed following the departure of juveniles Amsterdam albatross may illustrate the swift
2221 change in travel and movement behaviour, reflecting a more 'adult like' behaving, not indicating
2222 necessarily an improvement of flight performances and of the ability to cope with changing (i.e. increasing
2223 wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such as albatrosses.

2224 Both extrinsic (i.e. environmental conditions: variability in subtropical waters resources or in wind) and
2225 intrinsic (i.e. energetic demands linked to plumage renew) factors could be involved in the modulation of
2226 foraging behaviour, which can be reflected in the temporal variability ~~of activity parameters we found~~
2227 ~~whatever the stage~~. Subtropical environments in the southern Indian Ocean are generally characterized
2228 as oligotrophic areas but nonetheless are known to vary over the seasons. During the austral winter,
2229 colder surface waters and strong winds result in changes of oceanographic conditions associated with an
2230 increased primary productivity (Behera and Yamagata 2001; Terray 2011; Delord et al. 2021). Changes in
2231 water temperature associated with wind appear to result in seasonal biological production variations that
2232 affect seabirds (Delord et al. 2021), however, the delay between the increase in primary production and

2233 ~~the increase in potential prey for albatrosses is probably rather long in this oligotrophic context. These~~
2234 ~~changes were found to affect seabirds (Delord et al. 2021). Part of the activity changes observed following~~
2235 ~~the departure of juveniles Amsterdam albatross could reflect improvement of flight performances and of~~
2236 ~~the ability to cope with changing (i.e. increasing wind speed) wind conditions (Sergio et al. 2014), a key~~
2237 ~~parameter for soaring seabirds such albatrosses.~~

2238 In seabirds,

2239 ~~T~~emporal changes in foraging activities ~~were~~are often associated to the very strong contrast between
2240 reproduction and inter-breeding periods, shifting from high energetic needs linked to reproductive effort
2241 and associated constraints (i.e. central place foraging strategy; (Orlans and Pearson 1979)) to a reduction
2242 of these energetic constraints during the non-breeding period (sabbatical year for adults) (Williams 1966;
2243 Ricklefs 1977, 1983; Stearns 1992; Ydenberg et al. 1992). This contrast is particularly pronounced in
2244 seabirds (Mackley et al. 2010; Gutowsky et al. 2014) where energetic constraints play a decisive role in
2245 determining activity patterns (Phalan et al. 2007).

2246
2247 Molt is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996;
2248 Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in
2249 both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). ~~In large sized~~
2250 ~~albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding~~
2251 ~~season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch~~
2252 ~~1991).~~ Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting
2253 important constraints ~~that could compete with breeding (immature birds tend to renew fewer feathers~~
2254 ~~compared to adult breeders), and particularly in females (Weimerskirch 1991; see Supplementary). In~~
2255 ~~smaller sized seabirds, a link between moulting pattern and activity parameters was evidenced, resulting~~
2256 ~~in a clear temporal pattern partly explained by moult (Cherel et al. 2016).~~ Recently Gutowsky et al. (2014)

2257 suggested that tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes*
2258 albatrosses) could compromise flight from active wing moult during the non-breeding period and induce
2259 changes in daily activity budget during a 'quasi-flightless' stage. However, there is no such data for
2260 southern albatrosses. Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using
2261 GLS never suggested it such a compromise. However, adult birds during the non-breeding season appear
2262 to spend much more time on the water during winter, suggesting that partial moult may occur at this
2263 time, as observed in many other seabird species that have to moult during the non-breeding season and
2264 show reduced activity during specific periods that may correspond to moulting (Weimerskirch et al.
2265 2015b, 2020). Interestingly, immature appear to have this peak in time spent on the water in spring,
2266 suggesting different timing of moult.

2267
2268 Sex differences in activity

2269 Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross
2270 forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013;
2271 Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by
2272 differences in foraging habitats. We found support for the body-size hypothesis to explain sex differences
2273 in activity parameters, consistent with the important sexual dimorphism in the Amsterdam albatross.
2274 Males ~~did tend to spend~~ more numerous bouts on water whatever the stage, and depending on stage,
2275 shorter (juveniles only) compared to females. Consistently, we found that males ~~flew tended to fly~~ for
2276 longer periods (dry bouts duration) compared to ~~what females did~~. When considering all stages, males
2277 spent a higher percentage of time on water compared to females.

2278 Amsterdam albatross and its sister species the wandering albatross have a very close anatomy and similar
2279 use of the wind, although Amsterdam albatross is 5-8% smaller and 25% lighter (Barbraud et al.
2280 unpublished data. In the wandering albatross, due to sex differences in flight performance (specifically,

2281 due to their higher wing loading), males should both maintain longer flying effort and be more likely to
2282 minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). The change in
2283 foraging strategy, as in wandering albatross, tends to be dependent on breeding stage (Phalan et al. 2007;
2284 Louzao et al. 2014) leading to a greater use of the 'sit-and-wait' technique and may vary between sites,
2285 suggesting considerable behavioural plasticity (Phalan et al. 2007). This switch in foraging techniques
2286 could result in more frequent and shorter bouts on the water in the 'sit-and-wait' technique (compared
2287 to 'foraging-in-flight'). In other word, males may have more of a 'sit-and-wait' strategy while females have
2288 more of a 'foraging-in-flight' strategy, although there is some behavioural plasticity particularly over time.
2289 Our prediction that foraging behaviour differs between sexes was fully supported (i.e. sex-differences in
2290 activity parameters). Nevertheless, the similarity in time spent on the water suggests that the differences
2291 may be more subtle, showing some a trade-offs in duration and numbers between flying and water bouts.
2292 This trade-off should vary depending on stage as immature females tended to have shorter and more
2293 frequent bouts on the water. This implies that while probably feeding on similar water masses, the sexes
2294 might differ in type of prey targeted and/or used different foraging methods. The confirmation of this
2295 hypothesis reinforces the fact that the two-sibling species, as previously assumed, show a high degree of
2296 similarity in their foraging behaviour.
2297 Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex
2298 usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can
2299 result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey
2300 (Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019;
2301 Barbraud et al. 2021). It has also been suggested that size matters probably because the smaller and
2302 lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower
2303 wing loaded female wandering albatrosses, compared to males, are probably better able to exploit
2304 subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that

2305 females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than
2306 males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al.
2307 (2002); Stauss et al. (2012)).

2308

2309 Individual variability in activity

2310 There was inter-individual variability in almost all activity parameters whatever the stage considered. In
2311 juveniles, models indicated inter-individual variability in activity and in the rate of change of activity as a
2312 function of time elapsed since departure from the colony. Since the intercept terms in the models were
2313 significant, it seems as though individual variability (i.e., specialization on different foraging strategies)
2314 was a contributor to observed variability. However, the rate of change of intra-individual variation for
2315 some foraging strategies (percentage of time on water-number of flying bouts axis) oscillated during the
2316 juvenile period with a seemingly remarkable synchrony (see Fig S7). This suggests that changes in foraging
2317 behaviours occurred at the individual level during the juvenile period without stabilizing, at least during
2318 the first two years after fledging. This individual variability suggests development of specialized individual
2319 foraging behaviours (Harel et al. 2016; Rotics et al. 2016, 2021; Phillips et al. 2017). Nonetheless, given
2320 the small sample sizes these results should be interpreted with caution.

2321

2322 Conclusion

2323 Very few studies have investigated the ontogeny of foraging behaviour over such a long period of time,
2324 particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over
2325 several years. We investigated the foraging behaviour, through activity patterns, during the three life
2326 stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naïve juveniles,
2327 immatures and adults. Naïve juveniles during their first month at sea after leaving their colony exhibited
2328 lower foraging activity effort (greater proportion of time spent sitting on water, longer and more

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Mis en forme : Anglais (Royaume-Uni)

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2329 numerous bouts on water, and shorter and fewer flying bouts). Patterns of activity parameters in juveniles
2330 after independence suggested a progressive change of foraging performances during the first two months
2331 since fledging. Regardless of life stage considered, activity parameters exhibited temporal variability
2332 reflecting the modulation of foraging behaviour presumably. This variability is discussed (linked to both
2333 extrinsic (i.e. environmental conditions such as variability in food resources or in wind) and intrinsic (i.e.
2334 energetic demands linked to plumage renew during moult) factors). ~~We found sex differences in activity~~
2335 parameters according to time (month elapsed since departure from the colony and season
2336 month of the
2337 year), were consistent with the ~~important~~ sexual dimorphism in the Amsterdam albatross. It is therefore
2338 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.

2339

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Mis en forme : Anglais (Royaume-Uni)

2344 Nozahic. We are grateful to Richard Phillips, British Antarctic Survey, Cambridge for providing GLS loggers.

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Mis en forme : Anglais (Royaume-Uni)

Mis en forme : Police :Non Gras, Anglais (Royaume-Uni)

2351 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	1 st 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

2352 ¹ Stage/Age at which the individuals were equipped with loggers in our study

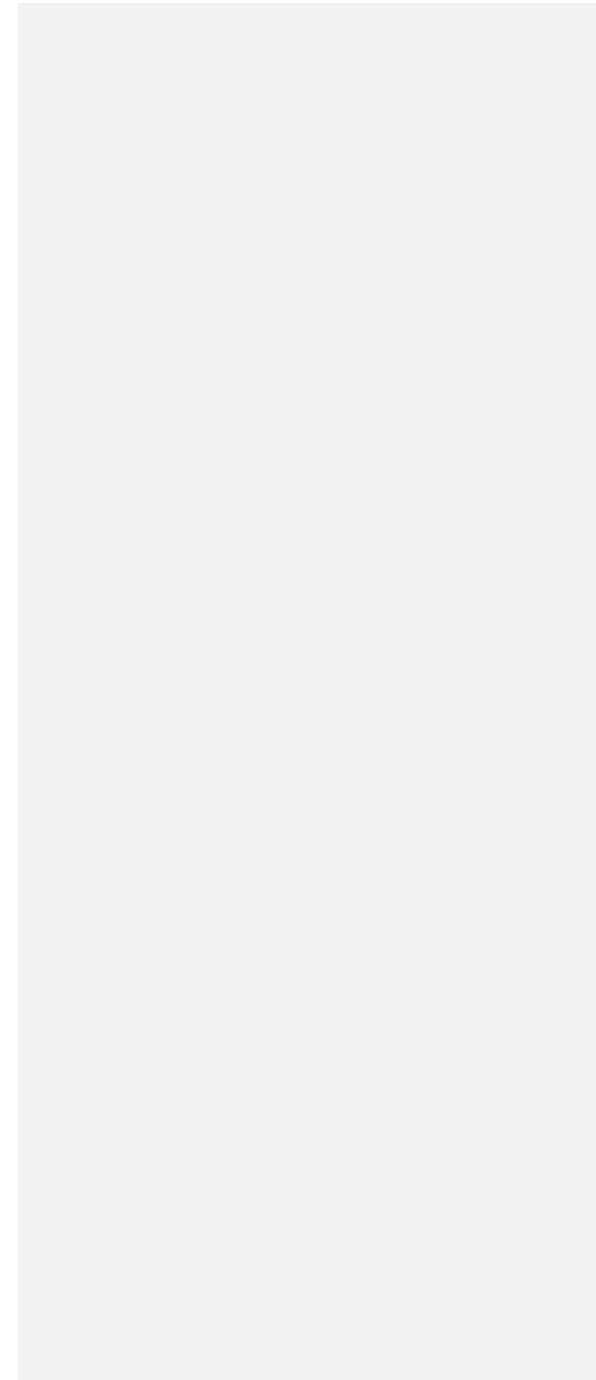
2353 Table 2 Sample sizes of birds tracked using Global Location Sensing (GLS) of Amsterdam albatross

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)

2354

2355 ¹ number of females F and males M, or not known NK for each stage

2356



2357 Table 3 Model selection for establishing variations in activity parameters of Amsterdam albatrosses in relation to sex, stage, number of months
 2358 spent since departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month
 2359 of the year (i.e. January and so on)

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

<u>Models</u>	<u>Fixed effects</u>	<u>Random effects</u>	<u>AIC</u>	<u>ΔAIC</u>
<u>Proportion of time spent on water (PC1S)</u>				
<u>M₀</u>	<u>Null model</u>		<u>28874.42</u>	<u>0</u>
<u>M₁</u>	<u>Month elapsed</u>	<u>Month elapsed: Individual</u>	<u>27311.97</u>	<u>1562.45</u>
<u>M₂</u>	<u>Month elapsed + Month</u>	<u>Month elapsed: Individual</u>	<u>26968.28</u>	<u>1906.14</u>
<u>M₃</u>	<u>Month elapsed + Month + Stage</u>	<u>Month elapsed: Individual</u>	<u>26889.23</u>	<u>1985.19</u>
<u>M₄</u>	<u>Month elapsed + Month + Stage + Sex</u>	<u>Month elapsed: Individual</u>	<u>26852.86</u>	<u>2021.56</u>
<u>Bouts spent on water (PC2S)</u>				
<u>M₀</u>	<u>Null model</u>		<u>26903.12</u>	<u>0</u>
<u>M₁</u>	<u>Month elapsed</u>	<u>Month elapsed: Individual</u>	<u>25803.80</u>	<u>1099.32</u>
<u>M₂</u>	<u>Month elapsed + Month</u>	<u>Month elapsed: Individual</u>	<u>25756.37</u>	<u>1146.75</u>
<u>M₃</u>	<u>Month elapsed + Month + Stage</u>	<u>Month elapsed: Individual</u>	<u>25751.47</u>	<u>1151.65</u>
<u>M₄</u>	<u>Month elapsed + Month + Stage + Sex</u>	<u>Month elapsed: Individual</u>	<u>25752.62</u>	<u>1150.50</u>
<u>Bouts spent dry -flying (PC3S)</u>				
<u>M₀</u>	<u>Null model</u>		<u>23042.26</u>	<u>0</u>

Tableau mis en forme

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

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

Mis en forme : Police : (Par défaut) Calibri

Tableau mis en forme

<u>M₁</u>	<u>Null model</u>	<u>Month elapsed: Individual</u>	<u>22540.25</u>	<u>502.01</u>
<u>M₂</u>	<u>Month elapsed</u>	<u>Month elapsed: Individual</u>	<u>22539.75</u>	<u>502.51</u>
<u>M₃</u>	<u>Month</u>	<u>Month elapsed: Individual</u>	<u>22509.79</u>	<u>532.47</u>
<u>M₄</u>	<u>Month + Stage + Sex</u>	<u>Month elapsed: Individual</u>	<u>22427.29</u>	<u>614.97</u>

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

Tableau mis en forme

Mis en forme : Police :(Par défaut) Calibri

Mis en forme : Police :(Par défaut) Calibri

2361

2362 Table 4 Values of activity parameters (mean ± sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam2363 albatross

2364

	<u>Juvenile¹</u>		<u>Juvenile²</u>		<u>Immature</u>		<u>Adult sabbatical</u>	
	<u>female</u>	<u>male</u>	<u>female</u>	<u>male</u>	<u>female</u>	<u>male</u>	<u>female</u>	<u>male</u>
<u>Time spent on water (%)</u>	<u>55.04 ± 20.46</u>	<u>58.18 ± 21.11</u>	<u>51.41 ± 19.18</u>	<u>52.88 ± 20.39</u>	<u>59.25 ± 21.53</u>	<u>63.31 ± 21.17</u>	<u>64.89 ± 20.90</u>	<u>69.98 ± 18.10</u>
<u>Wet bouts (sitting on water) duration (h)</u>	<u>1.21 ± 1.74</u>	<u>1.24 ± 1.76</u>	<u>1.16 ± 1.73</u>	<u>1.12 ± 1.59</u>	<u>1.07 ± 1.31</u>	<u>1.48 ± 2.12</u>	<u>1.47 ± 1.95</u>	<u>1.33 ± 1.96</u>
<u>Dry bouts duration (h)</u>	<u>1.29 ± 1.37</u>	<u>1.21 ± 1.32</u>	<u>1.34 ± 1.41</u>	<u>1.26 ± 1.40</u>	<u>1.32 ± 1.42</u>	<u>1.28 ± 1.55</u>	<u>1.44 ± 1.56</u>	<u>1.31 ± 1.42</u>
<u>Wet bouts (sitting on water) number</u>	<u>8.71 ± 4.01</u>	<u>8.76 ± 4.09</u>	<u>8.14 ± 3.85</u>	<u>8.48 ± 4.11</u>	<u>10.34 ± 4.29</u>	<u>8.59 ± 4.24</u>	<u>8.96 ± 3.98</u>	<u>10.28 ± 5.33</u>
<u>Dry bouts number</u>	<u>7.06 ± 3.20</u>	<u>7.27 ± 3.52</u>	<u>7.57 ± 3.21</u>	<u>7.85 ± 3.50</u>	<u>6.31 ± 3.21</u>	<u>5.75 ± 2.99</u>	<u>5.01 ± 2.64</u>	<u>4.64 ± 2.48</u>

2365 ¹ calculated during 28 months following departure; ² calculated during 9 months following departure

2366 Table 5 Model selection for establishing variations activity parameters for juveniles Amsterdam albatrosses in relation to sex, number of months
 2367 spent since departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month
 2368 of the year (i.e. January and so on)

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

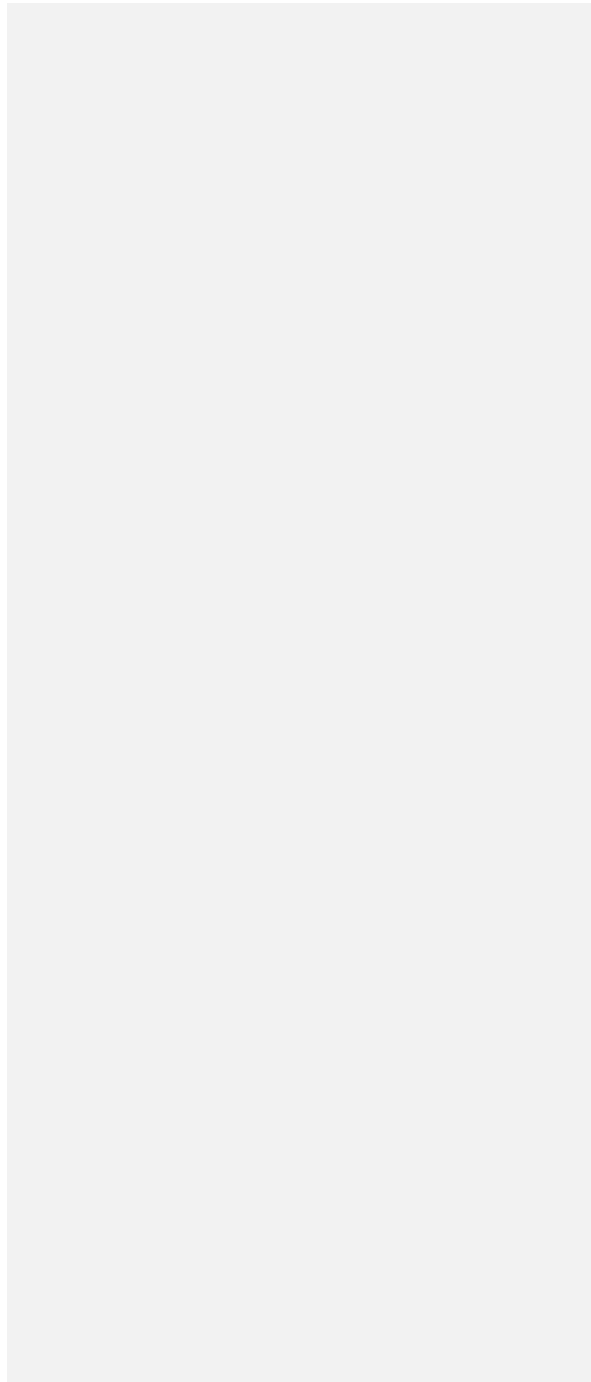
Tableau mis en forme

Mis en forme : Couleur de police : Noir

Mis en forme : Couleur de police : Noir

<u>Models</u>	<u>Fixed effects</u>	<u>Random effects</u>	<u>AIC</u>	<u>ΔAIC</u>
<u>Proportion of time spent on water (PC1J)</u>				
<u>M₀</u>	<u>Null model</u>		<u>22109.52</u>	<u>0</u>
<u>M₁</u>	<u>Month elapsed</u>	<u>Month elapsed: Individual</u>	<u>21864.11</u>	<u>245.41</u>
<u>M₂</u>	<u>Month elapsed + Month</u>	<u>Month elapsed: Individual</u>	<u>21625.69</u>	<u>483.83</u>
<u>Bouts spent on water (PC2J)</u>				
<u>M₀</u>	<u>Null model</u>		<u>20417.76</u>	<u>0</u>
<u>M₁</u>	<u>Month elapsed</u>	<u>Month elapsed: Individual</u>	<u>20072.42</u>	<u>345.34</u>
<u>M₂</u>	<u>Month elapsed + Month</u>	<u>Month elapsed: Individual</u>	<u>20004.65</u>	<u>413.11</u>
<u>M₃</u>	<u>Month elapsed + Month + Sex</u>	<u>Month elapsed: Individual</u>	<u>19999.00</u>	<u>418.76</u>
<u>Bouts spent dry -flying (PC3J)</u>				
<u>M₀</u>	<u>Null model</u>		<u>17708.47</u>	<u>0</u>
<u>M₁</u>	<u>Null model</u>	<u>Month elapsed: Individual</u>	<u>17548.75</u>	<u>159.72</u>
<u>M₂</u>	<u>Month elapsed</u>	<u>Month elapsed: Individual</u>	<u>17549.00</u>	<u>159.47</u>
<u>M₃</u>	<u>Month + Sex</u>	<u>Month elapsed: Individual</u>	<u>17541.02</u>	<u>167.45</u>

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



2370 Table 6 Body measurements of juveniles and adults Amsterdam albatross and percentage of differences between sexes for each measurement. Δ

2371 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
<u>Wing length (mm)</u>	<u>532.3 ± 62.1</u>	<u>543.6 ± 72.5</u>	<u>637.0 ± 13.3</u>	<u>654.7 ± 14.7</u>	<u>2.1</u>	<u>2.7</u>	<u>1.021</u>	<u>1.026</u>	<u>W=10554</u> <u>P<0.01</u>	<u>t₆₄=-4.882</u> <u>p<0.001</u>
<u>Tarsus length (mm)</u>	<u>113.1 ± 3.8</u>	<u>118.4 ± 3.8</u>	<u>112.4 ± 3.9</u>	<u>116.4 ± 4.0</u>	<u>4.5</u>	<u>3.5</u>	<u>1.047</u>	<u>1.077</u>	<u>t₂₂₉= -10.54</u> <u>p<0.001</u>	<u>t₂₈= -3.982</u> <u>p<0.001</u>
<u>Bill length (mm)</u>	<u>137.1 ± 4.0</u>	<u>143.1 ± 3.8</u>	<u>140.9 ± 4.7</u>	<u>145.0 ± 3.5</u>	<u>4.2</u>	<u>2.8</u>	<u>1.044</u>	<u>1.034</u>	<u>t₃₁₉= -13.89</u> <u>p<0.001</u>	<u>t₇₂= -4.268</u> <u>p<0.001</u>
<u>Bill depth (mm)</u>	<u>34.8 ± 3.4</u>	<u>36.9 ± 3.4</u>	<u>36.0 ± 1.5</u>	<u>38.0 ± 1.5</u>	<u>5.8</u>	<u>5.2</u>	<u>1.061</u>	<u>1.000</u>	<u>t₃₁₈= -5.629</u> <u>p<0.001</u>	<u>t₅₈= -4.821</u> <u>p<0.001</u>
<u>Body mass (g)</u>	<u>7719 ± 1228</u>	<u>8859 ± 1546</u>	<u>7509 ± 1561</u>	<u>7257 ± 1207</u>	<u>12.9</u>	<u>3.4</u>	<u>1.148</u>	<u>1.077</u>	<u>t₁₉₃=-5.846</u> <u>p<0.001</u>	<u>t₃₂=0.512</u> <u>p=0.612</u>

2372 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
 2373 (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
 2374 test)

2375 Table 7 Selected generalized linear models testing for the effect of sex and stage on body measurements
 2376 of Amsterdam albatross

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

2377
 2378 Table 8 GLM results for wing length of Amsterdam albatross modelled as a function of sex and stage
 2379 (GLM1). Reference values are female and adult. The degrees of freedom were 384

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

2380
 2381 Table 9 GLM results for tarsus length of Amsterdam albatross modelled as a function of sex and stage
 2382 (GLM2). Reference values are female and adult. The degrees of freedom were 296

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

2383 Table 10 GLM results for bill length of Amsterdam albatross modelled as a function of sex (GLM3).

2384 Reference values are female. The degrees of freedom were 393

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

2385

2386 Table 11 GLM results for bill depth of Amsterdam albatross modelled as a function of sex (GLM4).

2387 Reference values are female. The degrees of freedom were 378

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

2388

2389 Table 12 GLM results for body mass of Amsterdam albatross modelled as a function of sex and stage

2390 (GLM5). Reference values are female and adult. The degrees of freedom were 239

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

2391

2392

2393 Table 3 Values of activity parameters (mean \pm sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam

2394 albatross

2395

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

2396 ¹calculated during 28 months following departure; ²calculated during 9 months following departure

2397 **FIGURES**

2398 Figure 1 Modeled a) first and b) second axis of principal components analysis of activity parameters of all
2399 stages (i.e. adult, immature and juvenile) of Amsterdam albatrosses according to time elapsed (e.g.
2400 duration elapsed since departure from the colony expressed in month). Plain line corresponds to
2401 estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval.

2402
2403 Figure 2 Modeled a) first and b) second axis of principal components analysis of activity parameters of
2404 juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from
2405 the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model.
2406 Dotted lines indicate 95% confidence interval.

2407 Figure 1

2408

2409 Figure 2

2410

2411 Figure 3

2412

2413 Figure 4

2414

2415 Figure 5

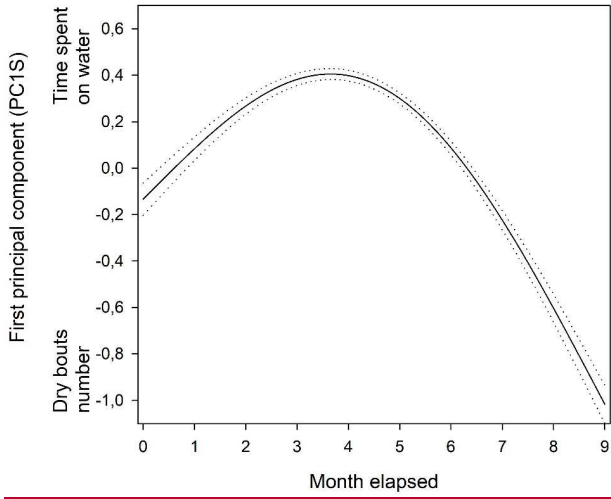
2416

2417 Figure 6

2418

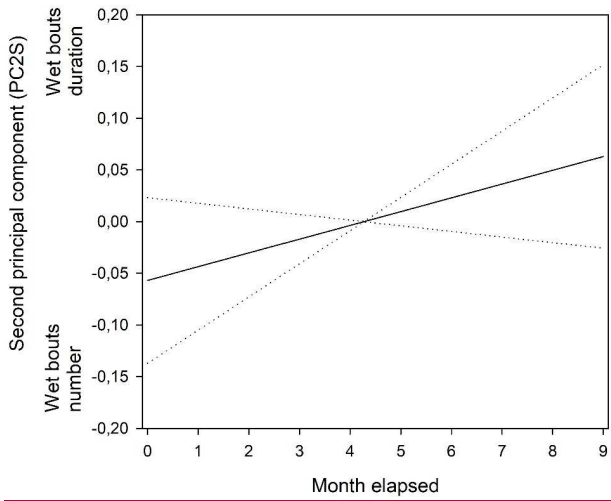
Mis en forme : Justifié

2419 Figure 1a

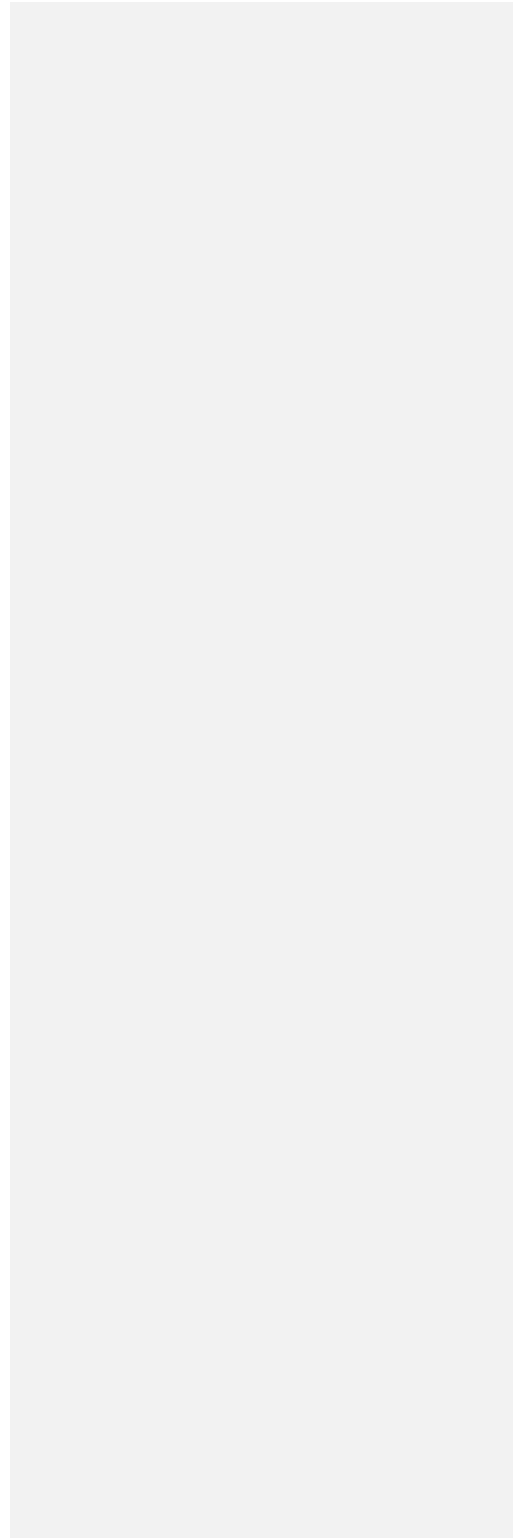


2420

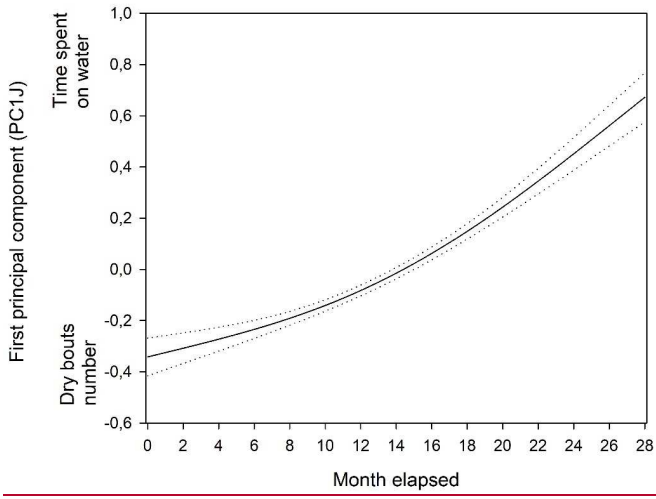
2421 Figure 1b



2422

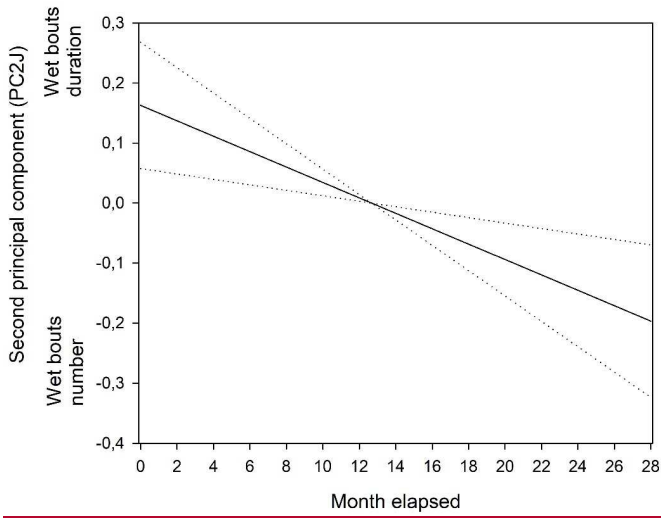


2424 Figure 2a

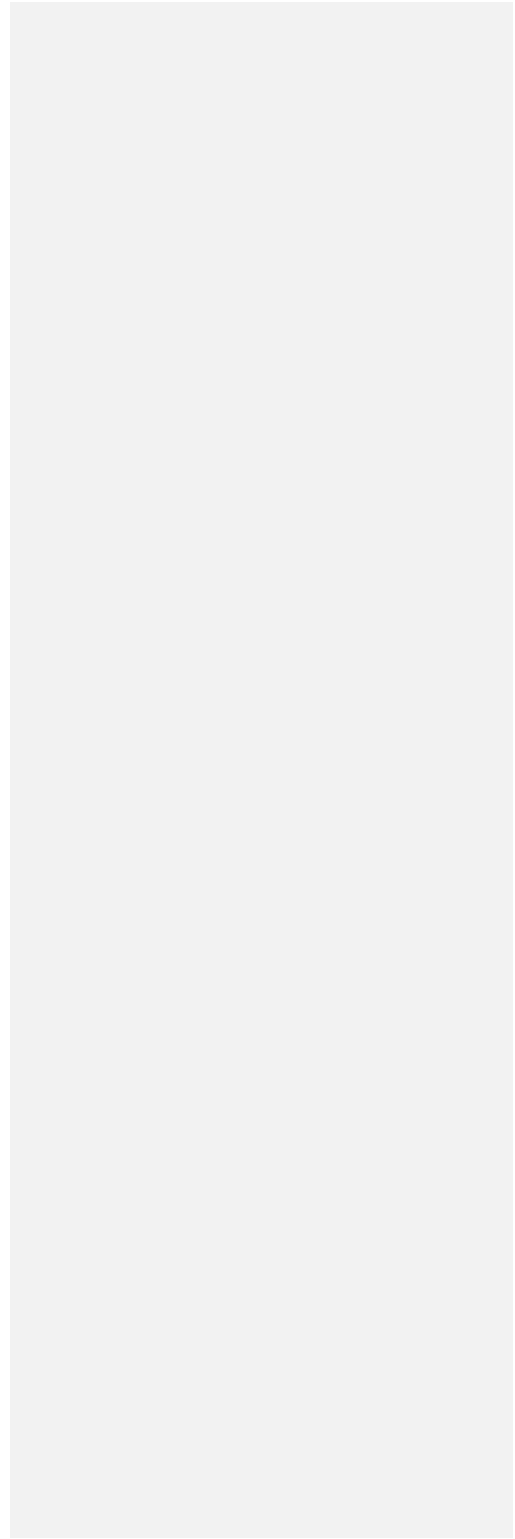


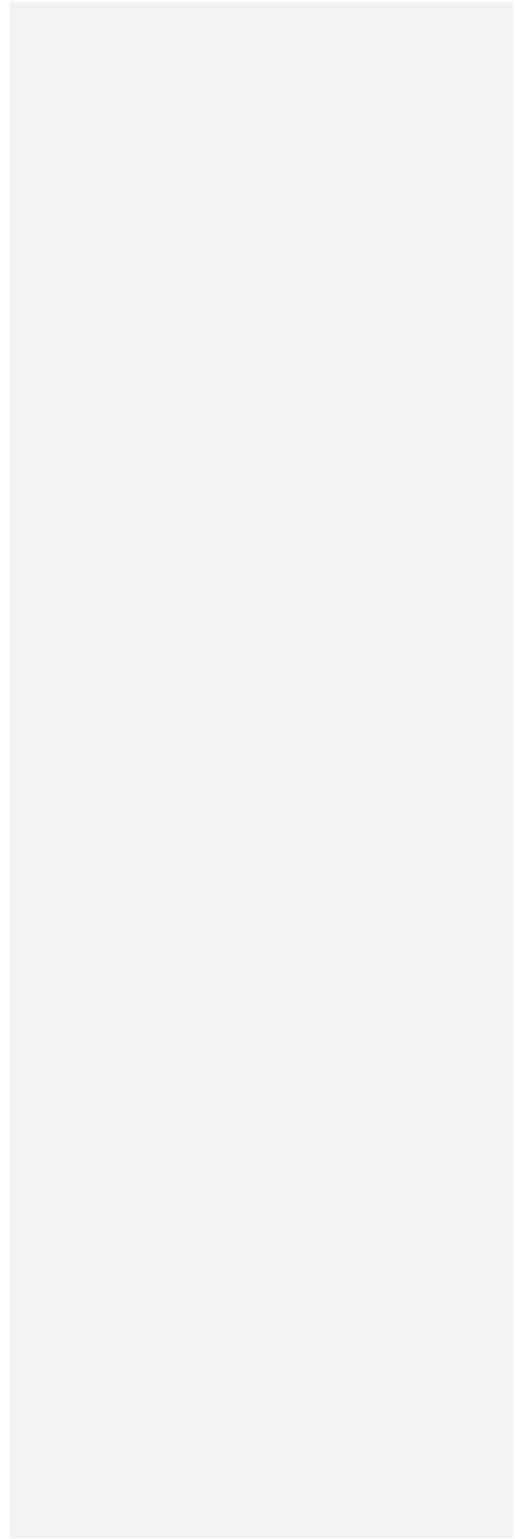
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2426 Figure 2b

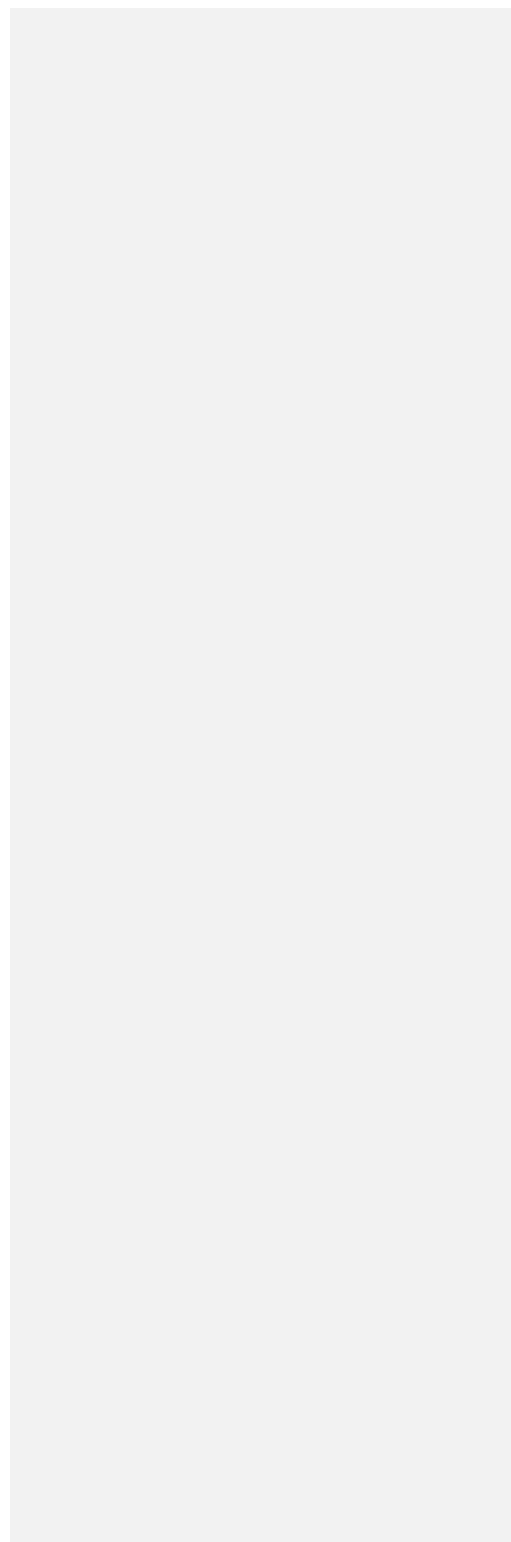


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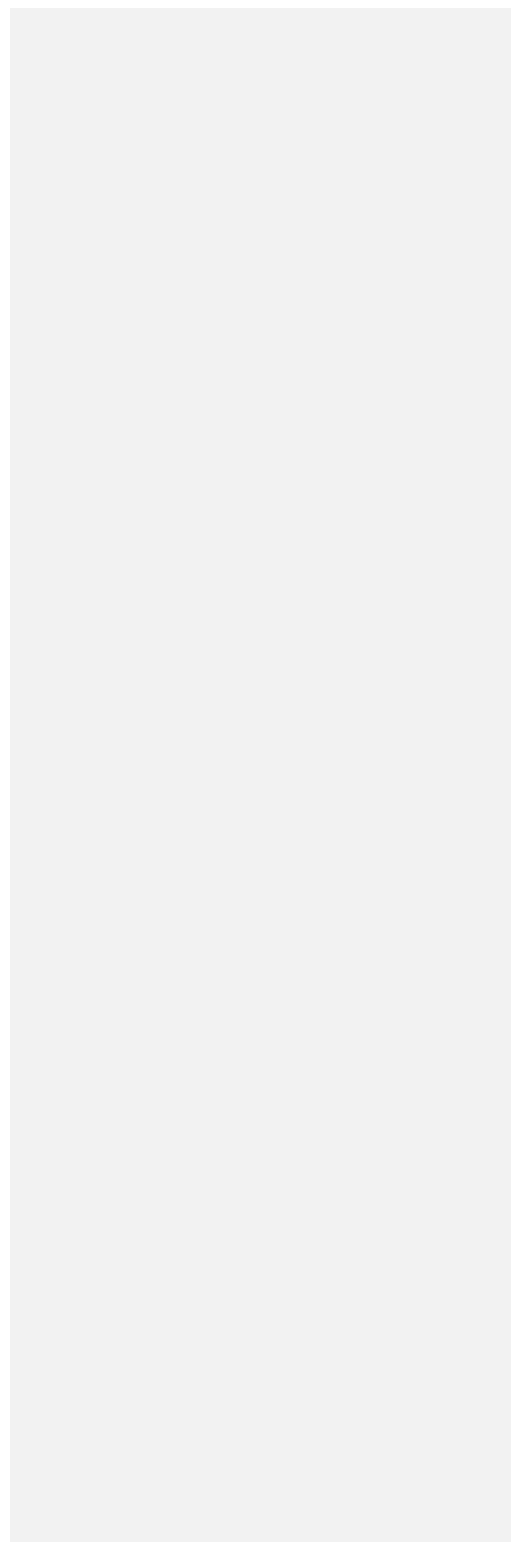




2430 **Figure 5**



2431 **Figure 6**



2432 **The authors of this article declare that they have no financial conflict of interest with the content of**
2433 **this article.**

2434

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2675

2676

2677 Supplementary

2678

2679 **Species biological aspects**

2680 Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to
2681 have very similar foraging behaviour compared to that of the wandering albatross, although subtle
2682 differences can appear (Pajot et al. 2021). Like other large albatross species (*Diomedea spp.*), the
2683 Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et
2684 al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive
2685 distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred
2686 as 'foraging-in-flight' is the lowest energy consuming feeding strategy for the wandering albatross
2687 (Weimerskirch et al. 1997). However, this strategy tends to change depending on breeding stage (Phalan
2688 et al. 2007; Louzao et al. 2014) leading to a more important utilization of the 'sit-and-wait' technique and
2689 possibly to vary depending on sites suggesting considerable behavioural plasticity (Phalan et al. 2007).
2690 This switch in foraging techniques could result in more frequent and shorter bouts on the water in the
2691 former technique (compared to 'foraging-in-flight').
2692 Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical
2693 period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale migratory movements
2694 reaching >4000 km from the colony exploiting continuously warm waters (~18°C). No clear longitudinal
2695 seasonality existed in the movements of adults, nonetheless they tended to move westwards in June/July
2696 and eastwards in November. The immature birds moved widely in longitude (0° to 135° E), exploiting
2697 exclusively warm waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity
2698 existed in the movements, except that they also tended to move westwards in June and eastwards in
2699 November. Juveniles exhibited very large post-fledging movement capacities over the southern Indian
2700 Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal

2701 gradient (27° to 47° S). Juveniles birds tended to move westwards first in March-April and temporarily
2702 exhibited synchronous individual movements. De Grissac et al. (2016) compared trajectories (i.e.
2703 departure direction or orientation toward specific areas) of juveniles and adults and showed that juveniles
2704 performed an initial rapid movement taking all individuals away from the vicinity of their native colony,
2705 and in a second time performed large-scale movements similar to those of adults during the sabbatical
2706 period. High individual variability and no clear differences between juveniles and adults patterns were
2707 found, except that adults foraged at significantly higher latitudes. De Grissac et al. (2016) concluded in an
2708 overlap in distribution between adults and juveniles due to the extensive area they used and their
2709 differences in latitudinal distribution compared to other Procellariiformes species.

2710
2711 Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996;
2712 Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in
2713 both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized
2714 albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding
2715 season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch
2716 1991). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting
2717 important constraints that could compete with breeding (immature birds tend to renew fewer feathers
2718 compared to adult breeders), and particularly in females (Weimerskirch 1991). In smaller sized seabirds,
2719 a link between moulting pattern and activity parameters was evidenced, resulting in a clear temporal
2720 pattern partly explained by moult (Cherel et al. 2016). Recently Gutowsky et al. (2014) suggested that
2721 tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could
2722 compromise flight from active wing moult during the nonbreeding period and induce changes in daily
2723 activity budget during a 'quasi-flightless' stage. However, there is no such data for southern albatrosses.
2724 Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested

2725 it such a compromise. However, adult birds during the non-breeding season appear to spend much more
2726 time on the water during winter, suggesting that partial moult may occur at this time, as observed in many
2727 other seabird species that have to moult during the non-breeding season and show reduced activity during
2728 specific periods that may correspond to moulting (Weimerskirch et al. 2015, 2020).

2729 Table S1 Hypotheses and predictions about the factors driving differences in activity (time spent on water, number and duration of flying bouts,
 2730 number and duration of water bouts) year-round in Amsterdam albatrosses
 2731

Hypothesis	Predictions		
	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
(AB) 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
(BC) 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 1 st 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 1 st 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 1 st 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) 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
<u>(D) Sex-specific body size</u>	<u>Behavioural difference maintained throughout the cycle: lower time spent on water for females compared to males</u> <u>Alternative prediction: no specific prediction due to trade-off between duration and number of bouts</u>	<u>Behavioural difference maintained throughout the cycle: females sustain shorter flying bouts but more numerous compared to males</u>	<u>Behavioural difference maintained throughout the cycle: females sustain longer water bouts duration but less numerous compared to males</u>

2733 Table S2 Selected models testing for the effects of sex, stage, number of months spent since departure (monthelap: duration elapsed since fledging
 2734 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
 2735 Amsterdam albatrosses

	Model #	Study variable ¹	Model structure	Sample size
All stages	gamm1	PC1S	$\sim s(\text{monthelap}, k = 2) + \text{monthf} + \text{stade} + \text{sex} + s(\text{monthelap}, \text{device_code}^2, \text{bs} = \text{"re"}) \sim s(\text{monthelap}, k=2, \text{bs}=\text{"cs"}) + \text{month} + \text{stage} + \text{sex}, \text{random} = \sim(1 + \text{monthelap} \text{device_code})$	8094
All stages	gamm2	PC2S	$\sim s(\text{monthelap}, k = 3) + \text{monthf} + \text{stade} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"}) \sim s(\text{monthelap}, k=3, \text{bs}=\text{"cs"}) + \text{month} + \text{stage} + \text{sex}, \text{random} = \sim(1 + \text{monthelap} \text{device_code})$	8094
All stages	gamm3	PC3S	$\sim \text{monthf} + \text{stade} + \text{sex} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"}) \sim s(\text{monthelap}, k=2, \text{bs}=\text{"cs"}) + \text{month} + \text{stage} + \text{sex}, \text{random} = \sim(1 + \text{monthelap} \text{device_code})$	8094
Juveniles	gamm4	PC1J	$\sim s(\text{monthelap}, k=2) + \text{monthf} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"}) \sim s(\text{monthelap}, k=2, \text{bs}=\text{"cs"}) + \text{month}, \text{random} = \sim(1 + \text{monthelap} \text{device_code})$	6161
Juveniles	gamm5	PC2J	$\sim s(\text{monthelap}, k = 2) + \text{monthf} + \text{sex} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"}) \sim s(\text{monthelap}, k=2, \text{bs}=\text{"cs"}) + \text{month} + \text{sex}, \text{random} = \sim(1 + \text{monthelap} \text{device_code})$	6161
Juveniles	gamm6	PC3J	$\sim \text{monthf} + \text{sex} + s(\text{monthelap}, \text{device_code}, \text{bs} = \text{"re"}) \sim \text{month} + \text{sex}, \text{random} = \sim(1 + \text{monthelap} \text{device_code})$	6161

2736 ¹ First, second and third principal component issued from principal components analyses considering i) all stages combined (PCS) and ii) only
2737 juveniles (PCJ); ² Individuals PROPWATER: proportion of time spent on water, WETBOOTS: bouts spent on water duration and number,
2738 DRYBOOTS: bouts spent dry-flying duration and numbe

Mis en forme : Police :Non Gras

Mis en forme : Police :Non Gras

2739 Table S3a GLMM-GAMM results for the first principal components, proportion of time spent sitting on
 2740 water (PROPWATERPC1S; GLMM1-gamm1 see Table S24) of Amsterdam albatross modelled as a
 2741 function of months spent since departure from the colony (month-elapf), and month of the year
 2742 (monthf), stage and sex. Reference values are 1st month spent at sea (month-elapf0) and January, adults
 2743 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

2744

	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

2745

2746

2747 Table S3b GLMM-GAMM results for the second principal components proportion of time spent sitting on
 2748 water (PROPWATERPC2S; GLMM1-gamm2 see Table S24) of Amsterdam albatross modelled as a
 2749 function of months spent since departure from the colony (month-elapf), ~~and~~ month of the year
 2750 ~~(monthf), stage and sex~~. Reference values are ~~1st month spent at sea (month-elapf0) and~~ January, adults
 2751 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

2752

	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

2753

2754

2755 Table S3c ~~GLMM-GAMM~~ results for the third principal components proportion of time spent sitting on
 2756 water (PROPWATERPC3S; GLMM1-gamm3 see Table S24) of Amsterdam albatross modelled as a
 2757 function of months spent since departure from the colony (month-elapf), ~~and~~ month of the year
 2758 ~~(monthf), stage and sex~~. Reference values are ~~1st month spent at sea (month-elapf0) and~~ January, adults
 2759 and females.

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

2760

	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

2761

2762

2763 Table S4a GLMM-GAMM results for the first principal components, proportion of time spent sitting on
 2764 water (PROPWATERPC1); GLMM1-gamm4, see Table S24 of juveniles Amsterdam albatross modelled as
 2765 a function of months spent since departure from the colony (month-elapf) and month of the year.
 2766 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

2767

	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

2768

2769

2770 Table S4b GAMM results for the second principal components proportion of time spent sitting on water
 2771 (PROPWATERPC2); GLMM1-gamm5 see Table S24) of juveniles Amsterdam albatross modelled as a
 2772 function of months spent since departure from the colony (month-elapf) and month of the year.
 2773 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

2774

	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

2775

2776

2777 Table S4c GLMM-GAMM results for the third principal components proportion of time spent sitting on
 2778 water (PROPWATERPC3); GLMM1-gamm5, see Table S24 of juveniles Amsterdam albatross modelled as
 2779 a function of months spent since departure from the colony (month-elap^f), month of the year and sex.
 2780 Reference value are 1st month spent at sea (month-elap^f0) and January and females.

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

2781

	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

2782

2783 **FIGURES**

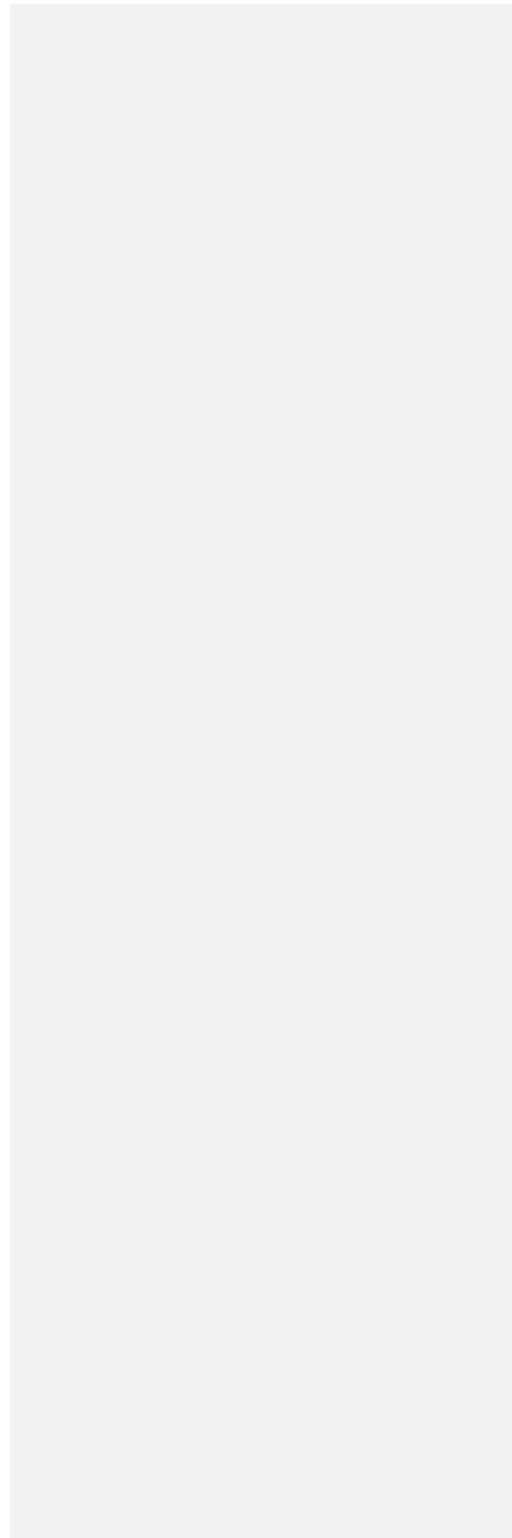
2784 ~~Figure S7 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony~~
2785 ~~for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars~~
2786 ~~represent ± 1 sd.~~

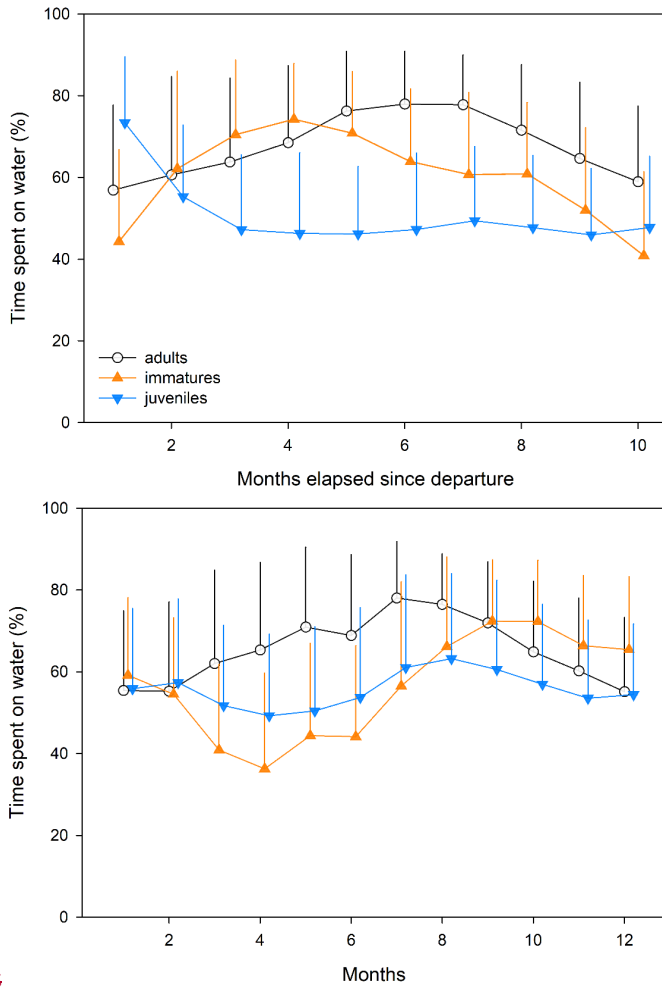
2787
2788 ~~Figure S8 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles,~~
2789 ~~immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd.~~

2790
2791 ~~Figure S9 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony~~
2792 ~~for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars~~
2793 ~~represent ± 1 sd.~~

2794
2795 ~~Figure S10 Daily wet bouts number (bouts on water) for every month since departure of the colony for~~
2796 ~~juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent~~
2797 ~~± 1 sd.~~

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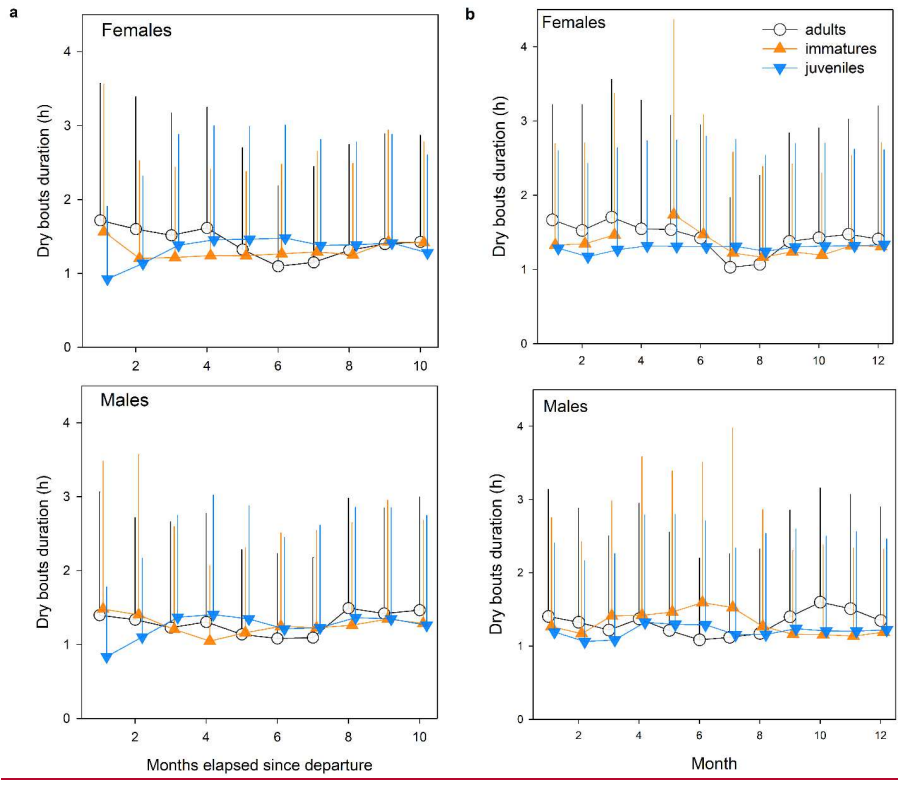




2799

S

2800 Figure S1 Daily proportions of time spent on water depending on stage (juveniles, immatures and adults)
 2801 for every month since departure from the colony (upper panel) and for each month of the year (lower
 2802 panel). Error bars represent ± 1 sd



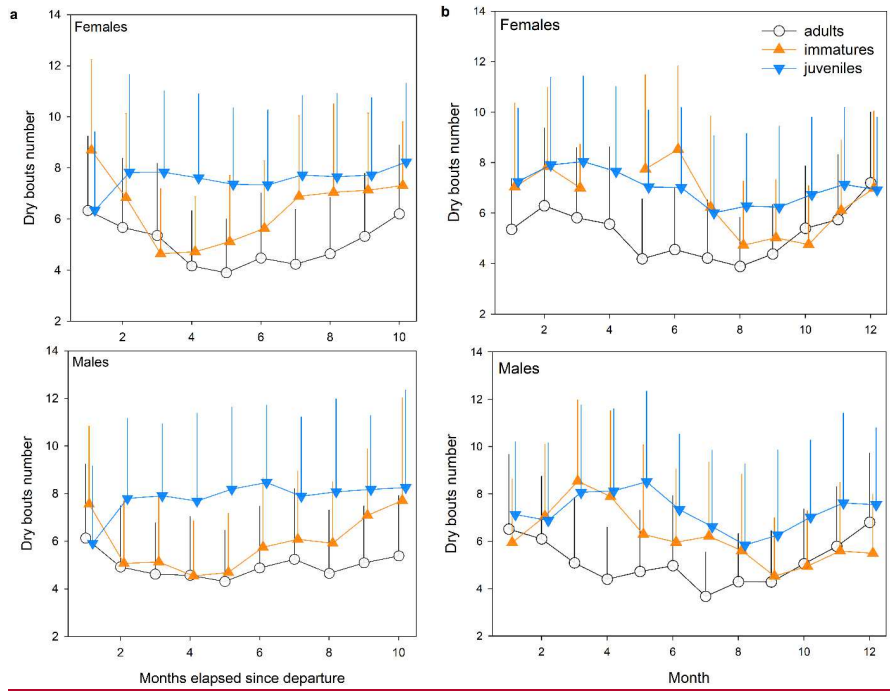
2803

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Figure S2 Daily flying bouts duration (dry bouts in hours) depending 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



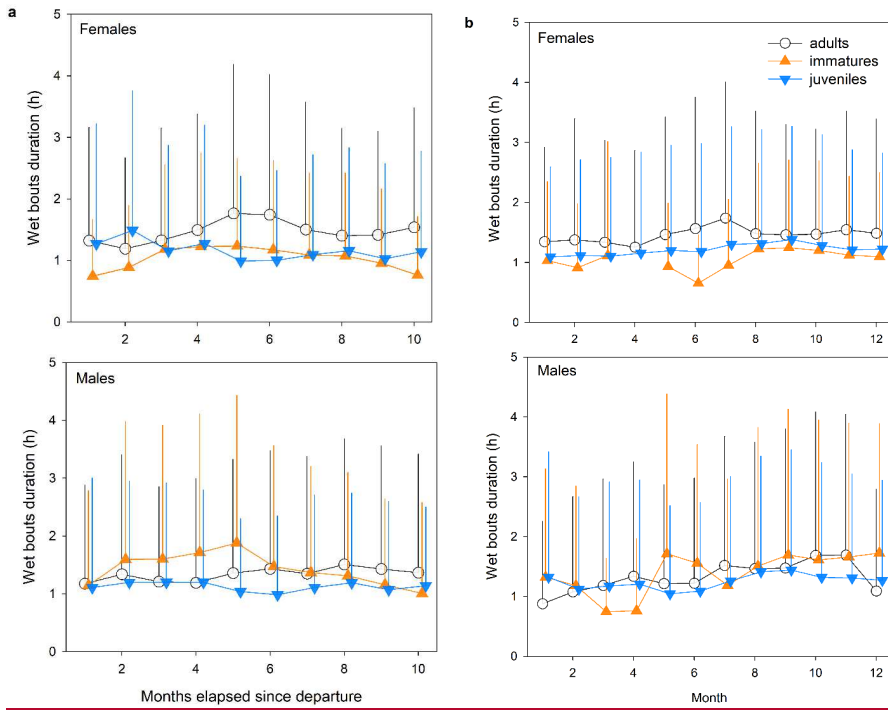
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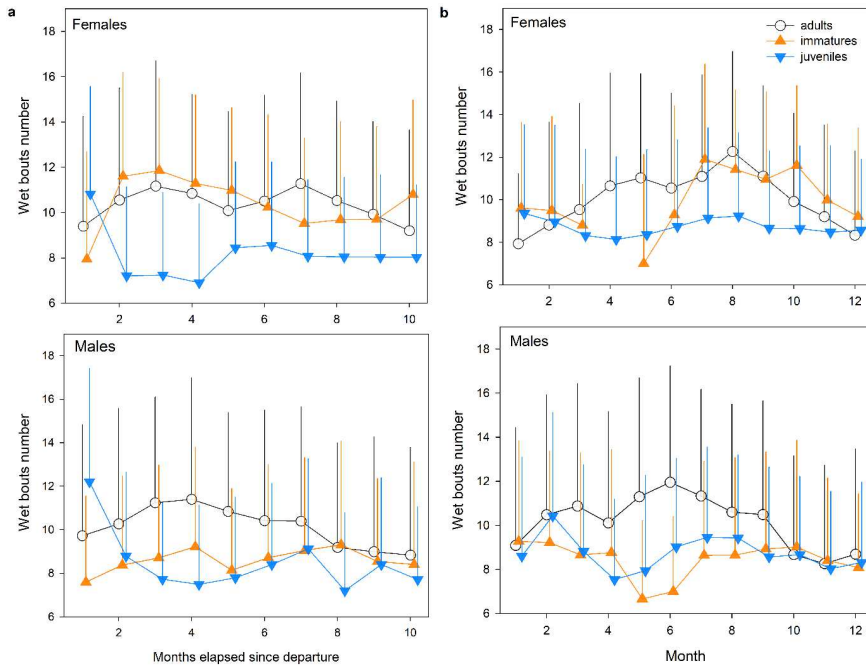
2810

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



2811

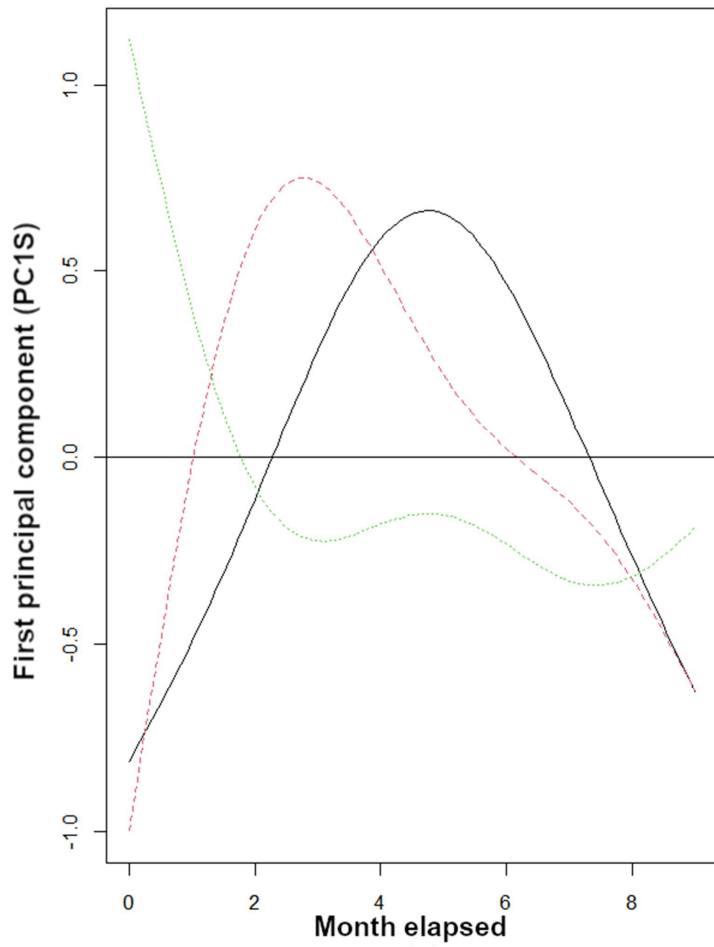
2812 Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures
 2813 and adults) and on sex (females and males) for every month since departure of the colony (upper panel)
 2814 and for each month of the year (lower panel). Error bars represent ± 1 sd



2815

2816 Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for
 2817 juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent
 2818 ± 1 sd

2819

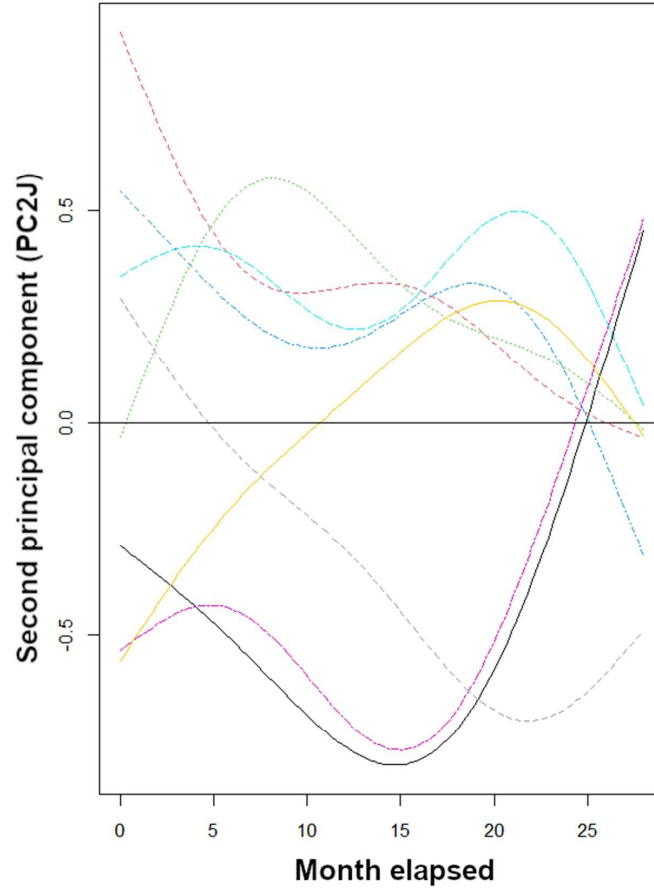
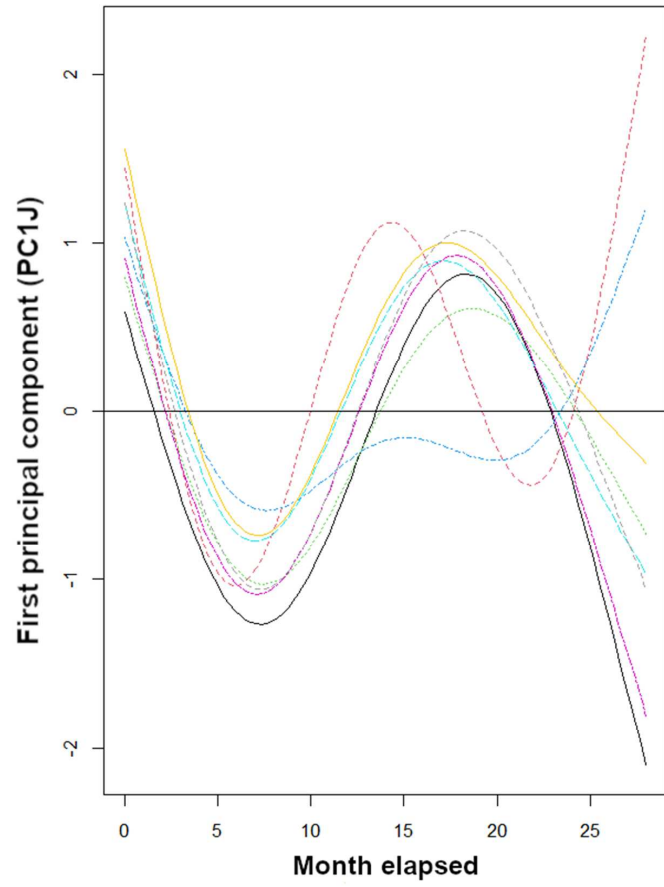


2820

2821 [Figure S6](#) Modeled first axis of principal components analysis of activity parameters of all stages (i.e. adult
 2822 (plain black line), immature (dashed red line) and juvenile (dotted green line)) of Amsterdam albatrosses
 2823 according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month).
 2824 Plain line corresponds to estimated smoother from the GAMM model

2825

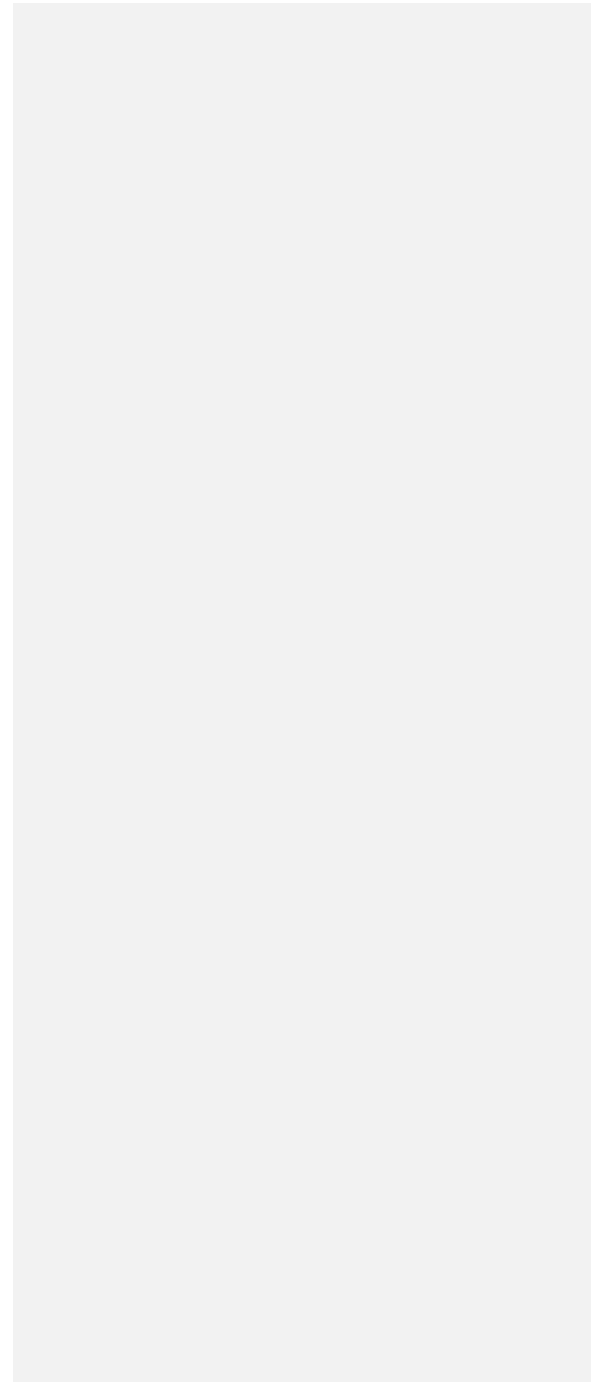
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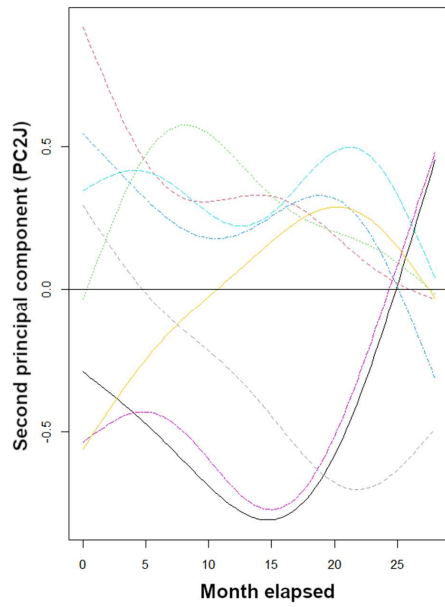
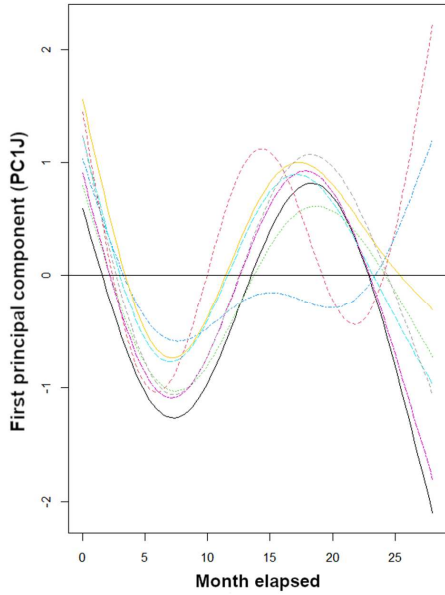


Mis en forme : Largeur : 27,94 cm, Hauteur : 21,59 cm

2827

2828 Figure S7 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of Amsterdam
2829 albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs obtained using
2830 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

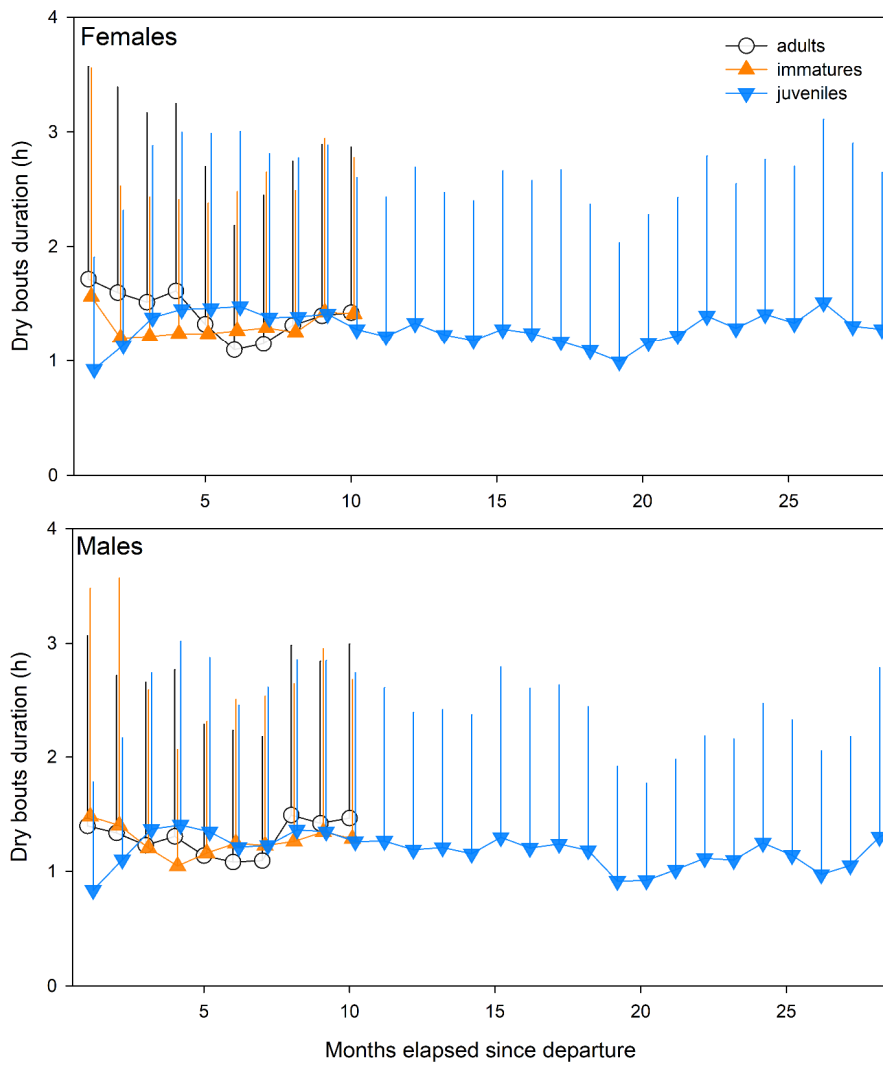


Figure S87. Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

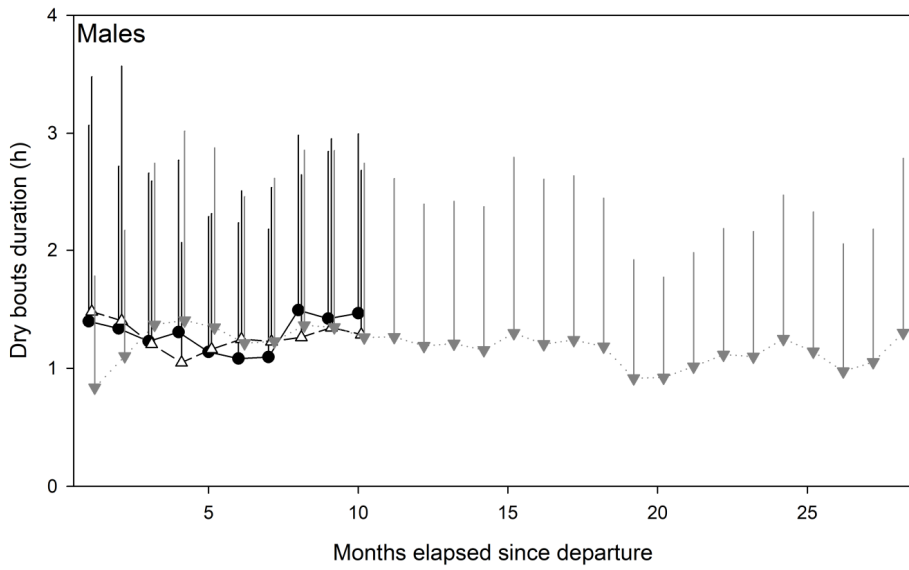
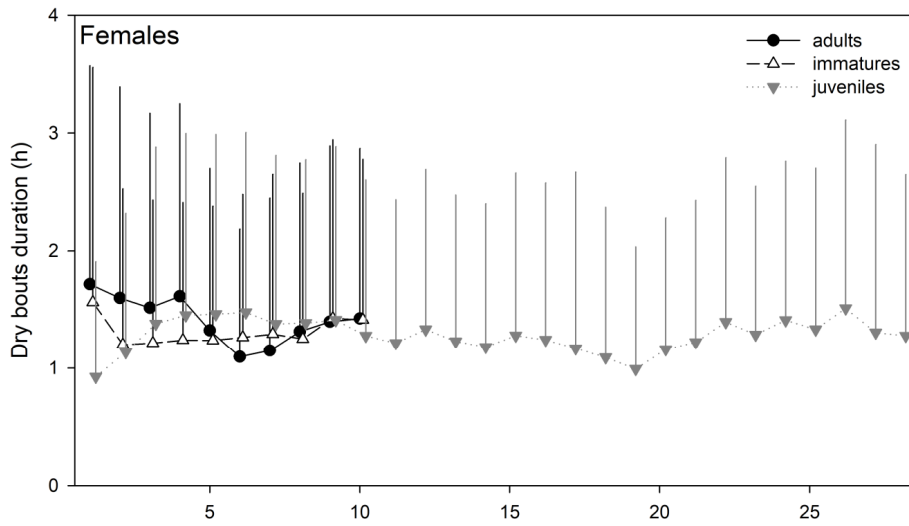


Figure S2

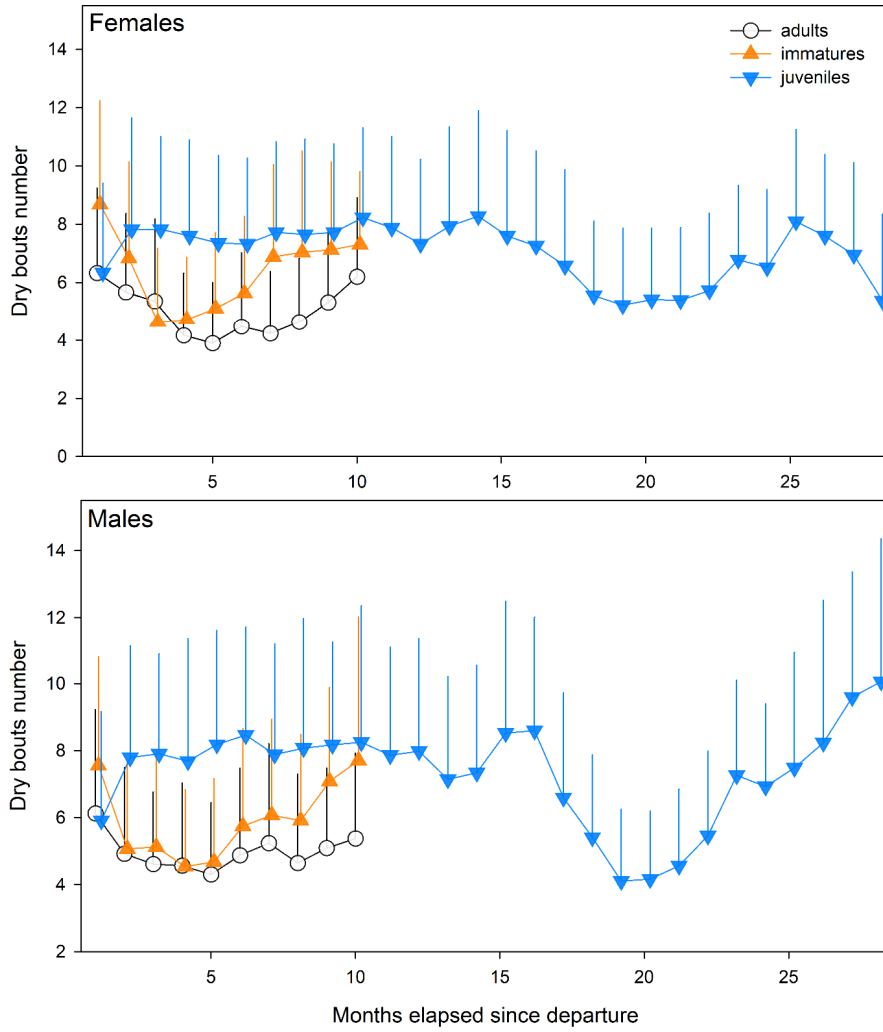


Figure S98. Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

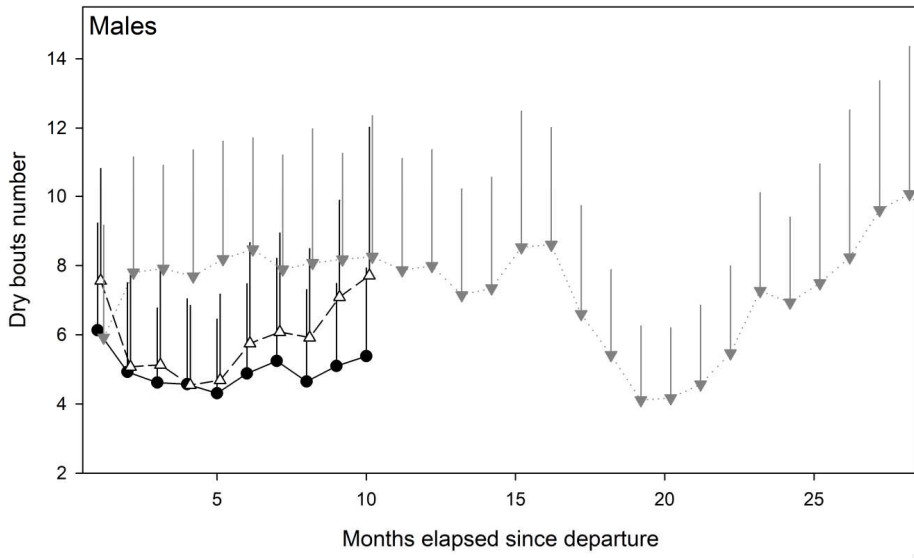
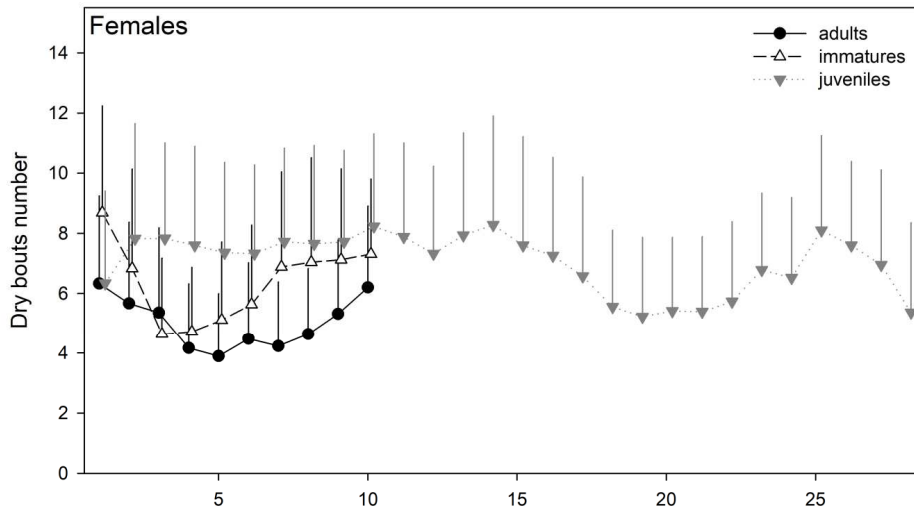
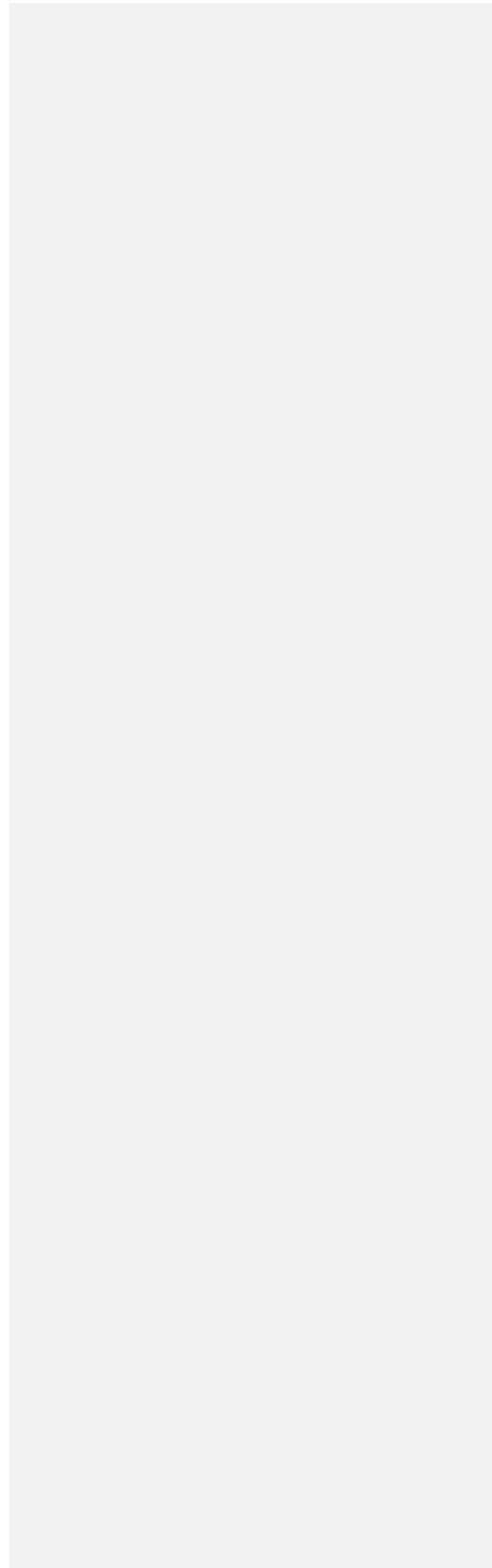
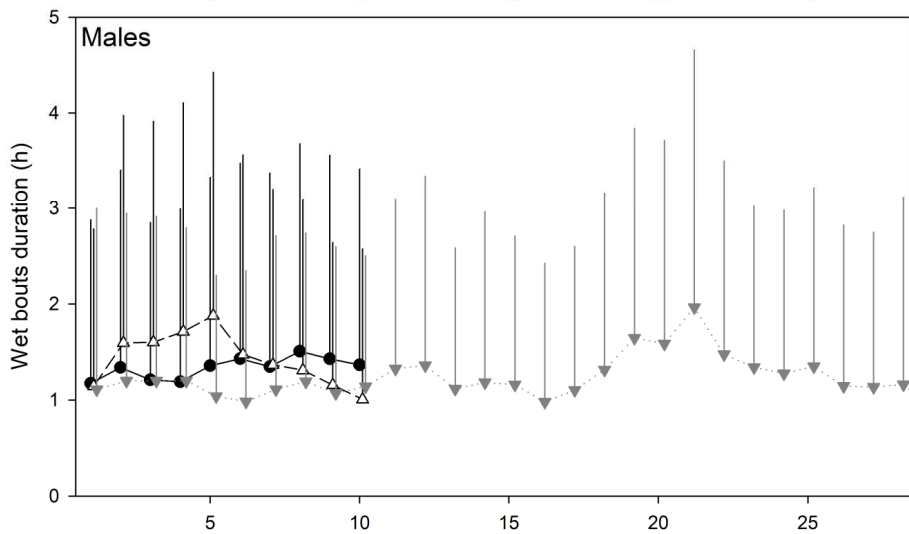
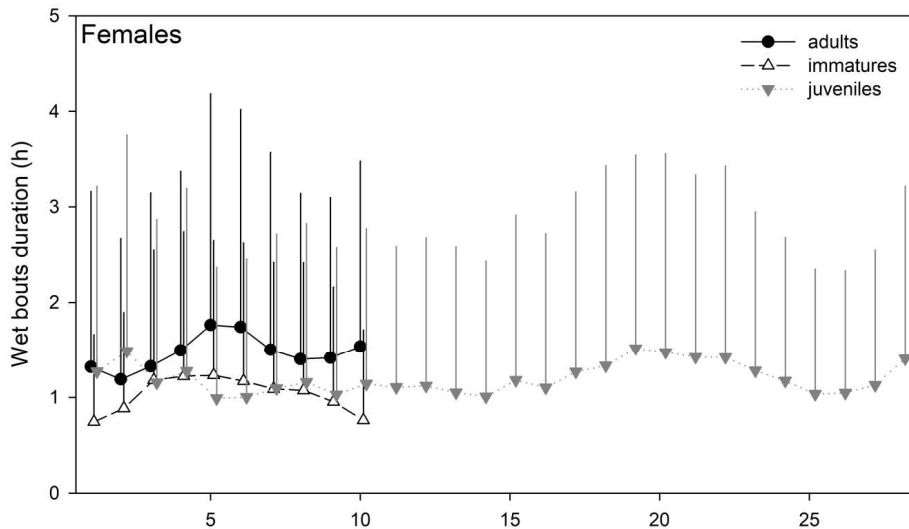


Figure S3





Months elapsed since departure

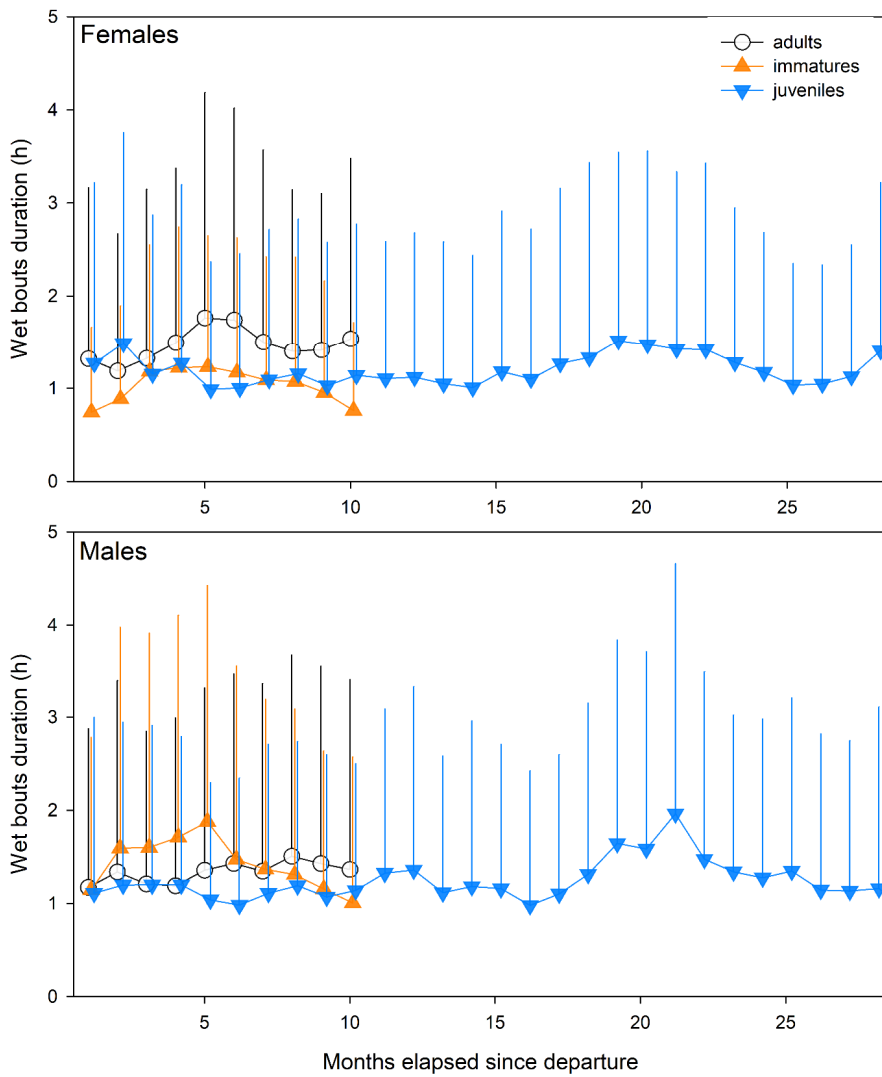


Figure S109 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

Figure S4

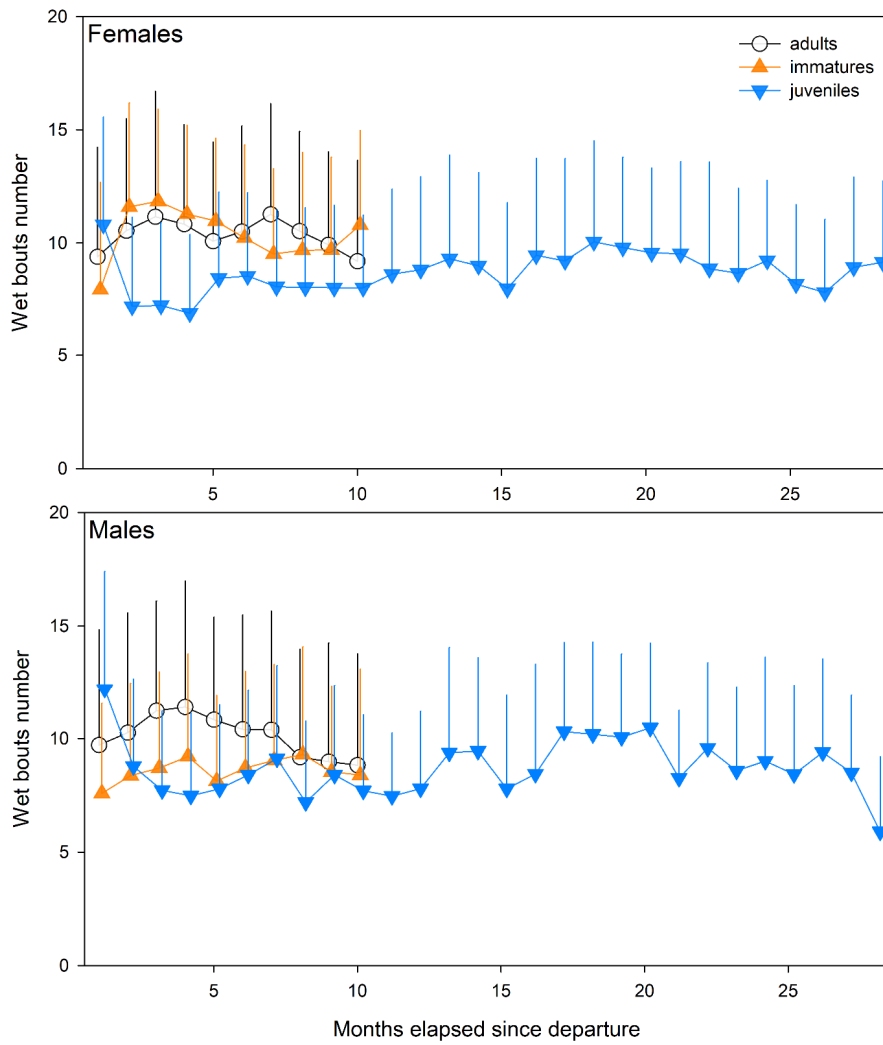


Figure S119 Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

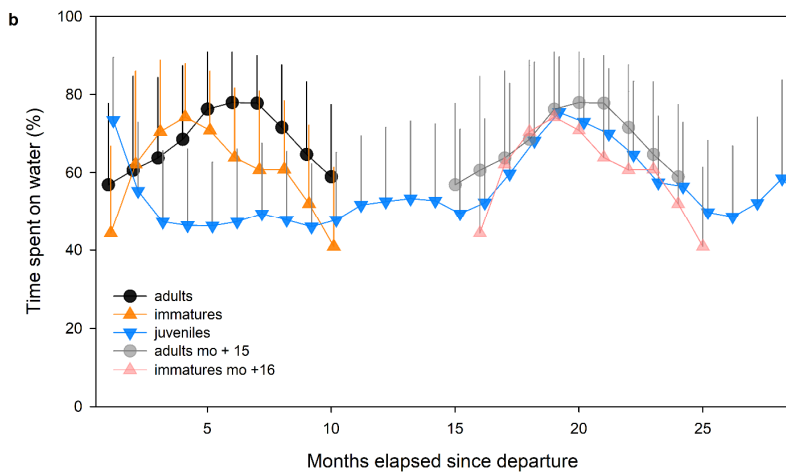
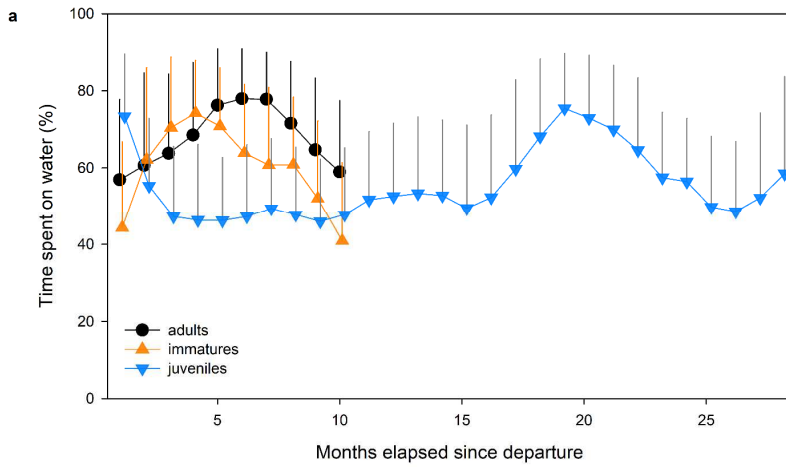
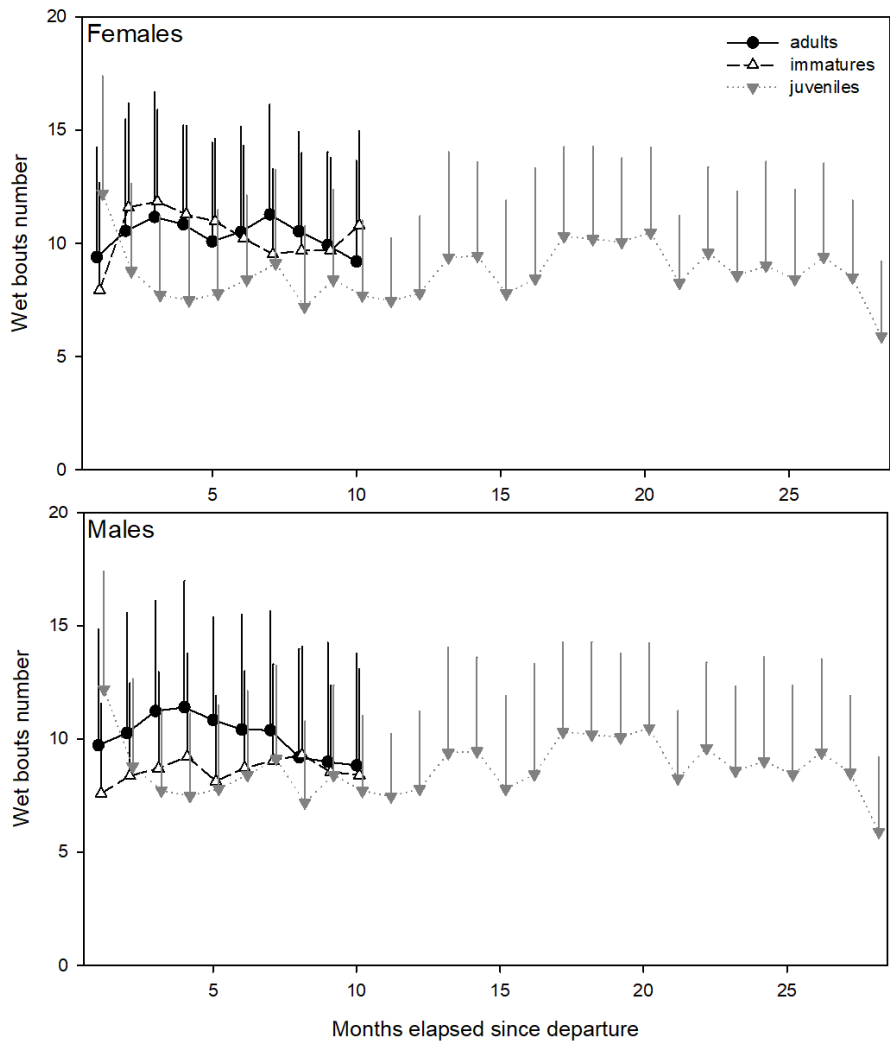


Figure S124 Daily proportions of time spent on water for every month since departure of the colony for juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel) and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error bars represent ± 1 sd



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