

1 **TITLE**

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

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9

10 **Abstract**

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

34

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

36 *Diomedea amsterdamensis*

37

## 38 **Introduction**

39 The transition from parental food dependency to independent foraging represents an important  
40 developmental stage in the life cycle of most vertebrate animals (Mushinsky et al. 1982; Margrath and Lill  
41 1985; Martin and Bateson 1985; Marchetti and Price 1989; Langen 1996; Burns et al. 2004) and is  
42 increasingly documented in a wide range of taxa (reptiles, birds, and some mammals). Juveniles differ  
43 from adults in various life history traits and tend to survive less well than adults in most long-lived animals  
44 (Ydenberg 1989; Menu et al. 2005; Oppel et al. 2015; Cheng et al. 2019). Several hypotheses have been  
45 proposed to explain higher mortality observed for young individuals compared to adults (Healy et al.  
46 2019). One of the most widely accepted hypotheses is inadequate/inferior foraging skills compared to  
47 adults, young naive individuals combining lack of experience and physical immaturity (Lack 1954; Daunt  
48 et al. 2007). Thus, a change in behaviour, resulting in an improvement of skills acquired from increasing  
49 experience is expected to occur during a period of learning through the immaturity phase. Such a learning  
50 process has been studied on various taxa from insects to primates (Bruner 1972; Caubet et al. 1992; Dukas  
51 2006; Rapaport and Brown 2008).

52 Juvenile birds are known to undertake vagrant erratic journeys during the post-fledging period especially  
53 in raptors (Urios et al. 2010; Krüger et al. 2014; Harel et al. 2016) and in seabirds (Riotte-Lambert and  
54 Weimerskirch 2013; Collet et al. 2020). Recent studies highlighted that the flight capacities and foraging  
55 behaviour of juveniles differed from those of adults in storks (Rotics et al. 2016), raptors (Harel et al.  
56 2016; Nourani et al. 2020) or seabirds (Ydenberg 1989; Péron and Grémillet 2013; de Grissac et al. 2017;  
57 Corbeau et al. 2020). Most flight components were found to improve over time to tend towards those of  
58 adults (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2017; Corbeau et al. 2020).

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

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

65 The Amsterdam albatross *Diomedea amsterdamensis* is a large and long-lived pelagic seabird with an  
66 extended immaturity stage (~ 9 years Rivalan et al. (2010)). Similarly to a closely related species, the  
67 wandering albatross *D. exulans*, their foraging strategy relies on very low flight costs as a result of their  
68 dynamic soaring flight, whereby individuals optimize the orientation of their movement with wind  
69 direction to maximize the daily distance covered (Pennycuik 1982). During initial post-fledging dispersal  
70 juveniles disperse alone over very long distances from their colony. At sea distribution during every stage  
71 of the life-cycle of Amsterdam albatross was studied by Thiebot et al. (2014) and De Grissac et al. (2016)  
72 who compared movement patterns of juveniles and adults, namely trajectories (i.e. departure direction  
73 or orientation toward specific areas). Both studies concluded on slight differences among stages in  
74 distribution due to the extensive area they used. However, foraging behaviour is known to be constrained  
75 by intrinsic factors such as sex, age, reproductive status and body size across a wide range of taxa and  
76 hence play a key role in shaping activity (King 1974; Alerstam and Lindström 1990; Wearmouth and Sims  
77 2008). To understand the potentially changes in foraging proficiency according to experience (life-history  
78 stages), longitudinal studies of individuals spanning critical periods of their lives are thus required.  
79 Advances in animal-borne instrumentation enable key component of foraging behaviour such as foraging  
80 effort and activity to be recorded over long periods.

81 In this study, we compare the foraging behaviour, through activity patterns, of naive juveniles (first years  
82 of independence at sea), immatures (individuals that never bred, age 2-10 years) and adults (individuals  
83 that bred at least once, age 8-28 years) of Amsterdam albatross (Table 1). By using miniaturized activity  
84 loggers to infer foraging behaviour (activity) throughout the successive life stages we addressed the  
85 following questions: i) do individuals belonging to different life-stages behaved differently? ii) are there

86 differences in activity patterns between life-stages, namely time spent on water and flying bouts, and are  
87 there detectable progressive changes?

88 Previous knowledge of the ecology of large albatrosses and Amsterdam albatross described above  
89 provides a practical framework for testing predictions about variability in foraging behaviour associated  
90 with sex, stage, time elapsed since departure from the colony and seasons which are summarised in Table  
91 S1. Given the overlap of spatial distribution between life-stages (Thiebot et al. 2014; de Grissac et al. 2016;  
92 Pajot et al. 2021) we predicted that juveniles would compensate for any lack of foraging proficiency by  
93 increasing foraging effort and time (i.e. lower time spent on water and longer flying bouts, in other words  
94 decreasing time sitting on water and longer and more numerous bouts in flight; Hypothesis (B), Table 2).  
95 We also predict sharp changes in activity following fledging of juveniles from the colony followed by more  
96 progressive changes. Based on results found on fledglings wandering albatross (Riotte-Lambert and  
97 Weimerskirch 2013; Pajot et al. 2021) showing that juveniles reached some adult foraging capacities in  
98 less than two months, we predicted that important changes should be detected in activity parameters  
99 early after the juvenile left the colony (within few first months). Overall, juveniles should show higher  
100 foraging effort compared to other life-stages (i.e. lower time spent on water, longer flying bouts and  
101 shorter water bouts). Due to seasonal changes in food availability individuals will face at sea after leaving  
102 the colony and the alleviation of energetic constraints linked to reproduction (for breeding adults) or to  
103 alternate foraging trips at sea and period on land for pair bonding and mating display (for immature birds),  
104 we predict that adjustments of activity will occur according to the time spent (i.e. in months elapsed) since  
105 the departure of individuals from the colony (Hypothesis (C), Table 2). In juveniles, we predict early and  
106 rapid changes after fledging and then more progressive changes. Due to environmental changes occurring  
107 throughout the seasons we predict temporal (i.e. related to the month of the year) changes in activity  
108 parameters for all life-stages (Hypothesis (D), Table 2). Although food availability may be lower during  
109 winter, foraging effort may also be reduced when adults and immatures are moulting (Weimerskirch

110 1991). Lastly, due to sex differences in flight performances (Shaffer et al. 2001; Clay et al. 2020),  
111 specifically, due to their higher wing loading, males should both maintain longer flying effort, and be more  
112 likely to minimize the number of flying bouts than females. Thereupon, and based on results on wandering  
113 albatross (Riotte-Lambert and Weimerskirch 2013), similar pattern should be maintained outside the  
114 breeding period. We thus predict differences in foraging behaviour between sexes (i.e. time spent on  
115 water, duration and number of flying and water bouts; Hypothesis (A), Table 2).

116

## 117 **Materials and methods**

### 118 **Study species and data loggers**

119 Amsterdam Island (37° 50' S; 77° 33' E) is located in the subtropical part of the southern Indian Ocean.  
120 In this oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder  
121 sub-Antarctic waters (Belkin & Gordon 1996). The Amsterdam albatross, like other great albatrosses, is a  
122 biennial breeder (Roux et al. 1983; Jouventin et al. 1989), with high survival during juvenile, immature and  
123 adult phase (Rivalan et al. 2010). The adults that raised a chick successfully do not start a new breeding  
124 cycle after chick fledging, but remain at sea for a sabbatical period (~1 yr; Table 1). However, early failed  
125 breeders may start to breed the following year. Immature birds may visit the colony when they are 4–7  
126 yrs old, but generally only start breeding at 9 yrs old ( Table 1; Weimerskirch et al. 1997). Juvenile birds  
127 fledge and migrate independently from the adults in January (Table 1). Exact fledging dates were not  
128 known for juveniles but were assessed from activity pattern as juvenile birds land on water quickly after  
129 leaving the colony (Weimerskirch et al. 2006). Amsterdam albatrosses were monitored annually since  
130 1983 and all individuals were individually marked (numbered stainless steel and plastic engraved colour  
131 bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age (79 individuals since the  
132 beginning of the study) and chicks of the year were banded, weighed (body mass  $\pm$  50 g using a Pesola®

133 spring balance) and measured (wing length  $\pm$  1 mm with a ruler, tarsus length, bill length, and bill depth  $\pm$   
134 0.1 mm with calipers).

135 Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical  
136 period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale dispersal reaching >4000  
137 km from the colony exploiting continuously warm waters ( $\sim$ 18°C). No clear longitudinal seasonality existed  
138 in the movements of adults, nonetheless they tended to move westwards in June/July and eastwards in  
139 November. The immature birds moved widely in longitude (0° to 135° E), exploiting exclusively warm  
140 waters 17°-18° C. Similarly to adults no clear longitudinal seasonality synchronicity existed in the  
141 movements, except that they also tended to move westwards in June and eastwards in November.  
142 Juveniles exhibited very large dispersal capacities over the southern Indian Ocean after fledging (15° to  
143 135° E,  $\sim$  4500 km from the colony), through a large range of latitudinal gradient (27° to 47° S). Juveniles  
144 birds tended to disperse westwards first in March-April and temporarily exhibited synchronous individual  
145 movements. De Grissac et al. (2016) compared trajectories (i.e. departure direction or orientation toward  
146 specific areas) of juveniles and adults and showed that juveniles performed an initial rapid movement  
147 taking all individuals away from the vicinity of their native colony, and in a second time performed large-  
148 scale movements similar to those of adults during the sabbatical period. High individual variability and no  
149 clear differences between juveniles and adults patterns were found, except that adults foraged at  
150 significantly higher latitudes. De Grissac et al. (2016) concluded in an overlap in distribution between  
151 adults and juveniles due to the extensive area they used and their differences in latitudinal distribution  
152 compared to other Procellariiforme species.

153 Global Location Sensing (GLS) loggers were used to study activity of birds over periods lasting up to  $\sim$  2  
154 years. GLSs record the ambient light level every 10 min, from which local sunrise and sunset hours can be  
155 inferred to estimate location every 12 h (Wilson et al. 1992). Immersion loggers tested for saltwater  
156 immersion every 30 s, storing the number of samples wet (>0) at the end of each 10 min period. We used



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

168

#### 169 **Data processing**

170 The raw immersion data were values from 0 (no immersion or dry, in flight or sitting on the ground) to  
171 200 (permanently immersed in sea water or wet), indicating the number of 3 s periods during 10 min  
172 blocks when the sensor was immersed in saltwater. Loggers recorded proportion of time in seawater at  
173 10 min intervals, which we summarized as hours in the water per day (PROWATER; 10 min blocks  
174 immersion data > 0). This measure is a reliable proxy of foraging effort linked to foraging behaviour of the  
175 species which enters the water principally to forage (Weimerskirch and Guionnet 2002). Additionally, the  
176 duration of the bouts spent entirely immersed (10 min blocks immersion data = 200) was calculated daily  
177 (hereafter referred as WETBOUTS). Conversely, when birds are not on land, the time spent dry was  
178 interpreted as flying (and thus not feeding). The duration of the bouts spent entirely dry (10 min blocks  
179 immersion data = 0) was calculated daily (hereafter referred as DRYBOUTS). Additionally the numbers of  
180 bouts (bouts on water: WETBOUTSNB and bouts flying: DRYBOUTSNB) were obtained daily. Although the

181 loggers integrated activity within each 10 min block and so did not provide the exact timing of landings  
182 and take-offs, Phalan et al. (2007) found for comparative purposes that bouts defined as a continuous  
183 sequence of 0 values for flight (dry) and a sequence of values of 1 or greater for wet bouts, were suitable  
184 proxies for activity.

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

193

#### 194 **Statistical analyses**

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

197 To investigate the causes of variability of the activity parameters during 24h (sitting on water –  
198 PROPWATER, WETBOOTS and DRYBOOTS duration, WETBOOTSNB and DRYBOOTSNB numbers) we used  
199 generalized linear mixed-effects model. Month elapsed since departure, month of the year, sex and stage  
200 were included as fixed effects and individual identity was used as a random effect to account for pseudo-  
201 replication issues, since the same individual provided several values. Month elapsed since departure and  
202 month of the year were used to test for time variation in activity parameters. We considered the number  
203 of months elapsed since departure available for all individuals (28 months since departure for juveniles  
204 and 9 months since departure for immatures and adults). Thus, for all stages combined we considered the

205 lowest number of months elapsed since departure available (9 months since departure). We first ran  
206 models testing for variability in PROPWATER, WETBOUTS, DRYBOUTS, WETBOUTSNB and DRYBOUTSNB  
207 independently for each stage (juvenile, immature and adult) and then by combining all stages (see  
208 Supplementary B; Table S2).

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

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

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

222 Models investigating the causes of variability of WETBOUTS and DRYBOUTS (glmmPQL 1 to 8, Table S2)  
223 were fitted using the function “*fitdist*” from the package DHARMA to assess the fit of residuals to a Gamma  
224 distribution. In this case, we fitted final models with penalized quasi-likelihood using the glmmPQL  
225 function in the package MASS (Venables and Ripley 2002). This meant that model simplification could  
226 proceed only on the basis of marginal Wald t-tests produced in the model summary (Table S7a). We  
227 therefore refitted models without interactions (sex \* month.elapsed for models for juveniles), until all

228 remaining terms were significant (for models specifications and sample sizes see Supplementary material  
229 Appendix 1, Table S7b).

230 Multi-collinearity among covariates was assessed using variance inflation factors (GVIFs, *AEDForecasting*  
231 library in R (Zuur 2009)) and a cut-off value of 3 was used to remove collinear variables prior to modeling.  
232 Spatial and statistical analyses were performed using (R Core Team 2019). Values are means  $\pm$  SD.

233

## 234 **Results**

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

240 All stages exhibited clear temporal patterns in their activities, related to the time elapsed since their  
241 departure from the colony and showing seasonal changes (indicated by the month of the year) whatever  
242 the five-activity metrics considered (Figures 1-5; Supplementary B Tables S2-S7d). Juveniles showed  
243 strong temporal changes linked to the time elapsed since departure from the colony (Figure 1). From the  
244 first month since departure, there was a quick decrease in the proportion of time spent on sea surface  
245 (mean value for the 1<sup>st</sup> month:  $73.4 \pm 16.1\%$ , for the 3<sup>rd</sup> month:  $47.2 \pm 18.3\%$ ), in the duration of bouts on  
246 water (mean duration for the 1<sup>st</sup> month:  $1.21 \pm 1.93\text{h}$ , for the 6<sup>th</sup> month:  $0.99 \pm 1.42\text{h}$ ) and in the numbers  
247 of bouts on water (mean number for the 1<sup>st</sup> month:  $11.34 \pm 4.96$ , for the 3<sup>rd</sup> month:  $7.43 \pm 3.59$ ), but an  
248 increase in the duration of bouts flying (mean duration for the 1<sup>st</sup> month:  $0.89 \pm 0.97\text{h}$ , for the 3<sup>rd</sup> month:  
249  $1.38 \pm 1.45\text{h}$ ), and the numbers of bouts flying (mean number for the 1<sup>st</sup> month:  $6.18 \pm 3.14$ , for the 3<sup>rd</sup>  
250 month:  $7.86 \pm 3.11$ ). Although less pronounced, the activity (proportion of time spent on seawater, the  
251 duration of bouts on water and the numbers of bouts on water or flying; Supplementary B Tables S2) also

252 varied according to the month of the year with two distinct periods (from November to February-March  
253 and from April-May to October). Highest values in the proportion of time spent on seawater, duration of  
254 bouts on water and numbers of bouts flying tended to be observed from November to February-March  
255 (Figure 1; Supplementary B Table S3a). In immatures and in adults the temporal pattern, i.e. months since  
256 their departure from the colony, of the activity parameters appeared generally reversed compared to  
257 juveniles (Figures 1-5; Supplementary B Tables S2, S3a-d, S4a-d, S5a-d, S6a-d, S7a-d). For the proportion  
258 of time spent on sea surface, the duration and the number of bouts on water, values were low early after  
259 departure then increased during the following months to peak ~ 3-5 months later, and finally tended to  
260 decrease at the end of the period. The opposite pattern was observed for duration and number of bouts  
261 flying. Regarding the seasonal changes (i.e. months of the year; Figures 1-5; Supplementary B Tables S2,  
262 S3a-S7d), for immatures, the temporal pattern tended to differ for all activity parameters when compared  
263 to that of months elapsed since departure. This was not the case for adults which exhibited alike temporal  
264 patterns. Furthermore, temporal patterns varied differently by sex whatever the stage considered (Figures  
265 2-5; Table 3).

266

267 When taking into account all three stages (juveniles, immatures and adults), interactions between the  
268 variables months elapsed since departure and stage, and between month of the year and stage were  
269 highly significant when explaining all the parameters of activity (proportion of time spent on seawater,  
270 the duration of bouts on water or flying and the numbers of bouts on water or flying; Supplementary B  
271 Tables S2). Therefore the difference between on one hand juveniles, and on the other hand immatures  
272 and adults depended on the number of months spent at sea since departure from the colony but also on  
273 the month of the year (Figures 1-5). Juveniles had very contrasted temporal patterns for all the activity  
274 parameters and almost never reached values of activity parameters observed for immatures and adults  
275 (Tables 4, Supplementary B Tables S3d, S4d, S5d, S6d, S7d, Figures S1-S4). This was all the more

276 pronounced when considering the time spent on sea surface (Figure 1), the duration (Figure 4) or the  
277 numbers of bouts on water (Figure 5), and the numbers of flying bouts (Figure 3). Juveniles spent more  
278 time in flight, with more frequent bouts as early as the second to third months spent at sea after their  
279 departure. During the 9 first months spent at sea after departure all the activity parameters of juveniles  
280 differed in values and in patterns when compared to immatures or adults.

281

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

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

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

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

307

## 308 **Discussion**

309 Elucidating the transition to independence in early life stages is crucial for understanding the causes of  
310 higher juvenile mortality in long-lived species (Fay et al. 2015; Payo-Payo et al. 2016). By comparing  
311 changes in behaviour at sea and foraging parameters of juveniles up to 28 months after their departure  
312 at sea with those of immatures and adults in the Amsterdam albatross, we showed that juveniles differed  
313 from immatures and adults in their activity patterns. During the first month following their departure from  
314 the colony juveniles spent a greater proportion of time sitting on water, did longer and more numerous  
315 bouts on water, and shorter and less numerous flying bouts than immatures and adults. However, from  
316 the second month following departure from the colony this pattern reversed and the activity patterns of  
317 juveniles became similar to that of immatures and adults only 10 to 17 months after fledging depending  
318 on the activity parameter considered (see Figure 6). Together, these results suggest a progressive  
319 improvement of movement performances during the first two months since fledging. Juvenile naïve birds  
320 during their first month at sea after leaving their colony exhibited lower foraging effort (greater  
321 proportion of time spent sitting on water, higher duration and more numerous bouts on water, and lower  
322 duration and less numerous flying bouts). They reach values similar to those of immatures and adults 2 to

323 3 months after departure (except for the number of dry/wet bouts for which it took longer), suggesting a  
324 progressive improvement of foraging performances during the first two months since fledging. This  
325 suggests that juvenile individuals are therefore very likely to have poorer foraging skills during their first  
326 two months spent at sea. Since all stages of the Amsterdam albatross forage in the same water masses  
327 (see Thiebot et al. 2014), differences in foraging behaviour were not due to different oceanographic  
328 characteristics as observed in other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al.  
329 2020b). These lower performances could be due to a combination of lack of experience of optimal  
330 behaviours, poor knowledge of the environment, use of distinct cues and/or physical immaturity (Shaffer  
331 et al. 2001; Frankish et al. 2020a). It is likely that increasing exposure to diverse foraging situations allows  
332 juveniles to rapidly accumulate foraging experience and improve various aspects of foraging.

333 The lower performance of juveniles we found is consistent with studies on wandering albatrosses and  
334 Amsterdam albatrosses (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2017; Pajot et al. 2021)  
335 during the first weeks at sea, which found that shortly after fledging juvenile albatrosses employ similar  
336 foraging strategies as adults. Additional skills need to be acquired during the immature period before the  
337 efficiency of these behaviors matches that of adults. This is also typical of other seabird taxa, which show  
338 progressive improvement in flight performance with the numbers of days since fledging (Yoda et al. 2004;  
339 Mendez et al. 2017; Collet et al. 2020; Corbeau et al. 2020). For example juvenile brown boobies *Anous*  
340 *stolidus* improved their flight abilities (Yoda et al. 2004) and juvenile European shags *Phalacrocorax*  
341 *aristotelis* compensate for poor foraging success by increasing their foraging time during first months after  
342 fledging (Daunt et al. 2007). In contrast, flight capability (flight speed and sinuosity) comparable to that of  
343 adults allows juvenile white-chinned petrels *Procellaria aequinoctialis* to rapidly flew large distances from  
344 the colony (Frankish et al. 2020).

345 Notwithstanding the progressive improvement of movement performances (foraging parameters  
346 estimated from activity parameters improved with time elapsed) quantified in juvenile Amsterdam



347 albatrosses, it remains elusive whether this is a question of physical development and/or a matter of  
348 gaining experience.

349

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

362 Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to  
363 have very similar foraging behaviour compared to that of the Wandering albatross, although subtle  
364 differences can appear (Pajot et al. 2021). Although Amsterdam albatross is 5-8% smaller and 25% lighter  
365 than wandering albatross, the two species have a very close anatomy and similar use of the wind. In the  
366 wandering albatross, due to sex differences in flight performance, specifically, due to their higher wing  
367 loading, males should both maintain longer flying effort and be more likely to minimize the number of  
368 flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). Hence, wandering albatross is known to  
369 forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008).  
370 This strategy referred as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the

371 wandering albatross (Weimerskirch et al. 1997b). However, this strategy tends to change depending on  
372 breeding stage (Phalan et al. 2007; Louzao et al. 2014) leading to a more important utilization of the '*sit-*  
373 *and-wait*' technique and possibly to vary depending on sites suggesting considerable behavioural  
374 plasticity (Phalan et al. 2007). This switch in foraging techniques could result in more frequent and shorter  
375 bouts on the water in the former technique (compared to '*foraging-in-flight*'). In other word, males may  
376 have more of a '*sit-and-wait*' strategy while females have more of a '*foraging-in-flight*' strategy, although  
377 there is some behavioural plasticity particularly over time. Our prediction that foraging behaviour differs  
378 between sexes was fully supported (i.e. sex-differences in bouts duration and number). Nevertheless, the  
379 similarity in time spent on the water suggests that the differences may be more subtle, showing some a  
380 trade-offs in duration and numbers between flying and water bouts. This trade-off should vary depending  
381 on stage as immature females tended to have shorter and more frequent bouts on the water. This implies  
382 that while probably feeding on similar water masses, the sexes might differ in type of prey targeted and/or  
383 used different foraging methods. The confirmation of this hypothesis reinforces the fact that the two-  
384 sibling species, as previously assumed, show a high degree of similarity in their foraging behaviour.  
385 Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex  
386 usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can  
387 result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey  
388 (Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019;  
389 Barbraud et al. 2019). It has also been suggested that size matters probably because the smaller and  
390 lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001), suggesting that lighter and lower  
391 wing loaded female wandering albatrosses, compared to males, are probably better able to exploit  
392 subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that  
393 females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than

394 males. However, the sexual dimorphism hypothesis is not always clearly supported (e.g., Lewis et al.  
395 (2002); Stauss et al. (2012)).

396

397 Both extrinsic (i.e. environmental conditions: variability in subtropical waters resources or in wind) and  
398 intrinsic (i.e. energetic demands linked to plumage renew) factors could be involved in the modulation of  
399 foraging behaviour, which can be reflected in the temporal variability of activity parameters we found  
400 whatever the stage. Subtropical environments in the southern Indian Ocean are generally characterized  
401 as oligotrophic areas but nonetheless are known to vary over the seasons. During the austral winter,  
402 colder surface waters and strong winds result in changes of oceanographic conditions associated with an  
403 increased primary productivity (Behera and Yamagata 2001; Terray 2011; Delord et al. 2021). Changes in  
404 water temperature associated with wind appear to result in seasonal biological production variations,  
405 however, the delay between the increase in primary production and the increase in potential prey for  
406 albatrosses is probably rather long in this oligotrophic context. These changes were found to affect  
407 seabirds (Delord et al. 2021). Part of the activity changes observed following the departure of juveniles  
408 Amsterdam albatross could reflect improvement of flight performances and of the ability to cope with  
409 changing (i.e. increasing wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring  
410 seabirds such albatrosses.

411

412 Temporal changes in foraging activities were often associated to the very strong contrast between  
413 reproduction and inter-breeding periods, shifting from high energetic needs linked to reproductive effort  
414 and associated constraints (i.e. central place foraging strategy) to a reduction of these energetic  
415 constraints during the non-breeding period (sabbatical year for adults). This contrast is particularly  
416 pronounced in seabirds (Mackley et al. 2010; Gutowsky et al. 2014) where energetic constraints play a  
417 decisive role in determining activity patterns (Phalan et al. 2007).

418 Molt is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996;  
419 Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in  
420 both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). In large-sized  
421 albatrosses like Amsterdam albatross, replacement of primary feathers lasts for more than one breeding  
422 season, and the moult of primaries never occurs during the breeding season (Furness 1988; Weimerskirch  
423 1991). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting  
424 important constraints that could compete with breeding (immature birds tend to renew fewer feathers  
425 compared to adult breeders), and particularly in females (Weimerskirch 1991). In smaller sized seabirds,  
426 a link between moulting pattern and activity parameters was evidenced, resulting in a clear temporal  
427 pattern partly explained by moult (Cherel et al. 2016). Recently Gutowsky et al. (2014) suggested that  
428 tropical albatrosses (i.e. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses) could  
429 compromise flight from active wing moult during the nonbreeding period and induce changes in daily  
430 activity budget during a 'quasi-flightless' stage. However, there is no such data for southern albatrosses.  
431 Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested  
432 it such a compromise. However, adult birds during the non-breeding season appear to spend much more  
433 time on the water during winter, suggesting that partial moult may occur at this time, as observed in many  
434 other seabird species that have to moult during the non-breeding season and show reduced activity during  
435 specific periods that may correspond to moulting (Weimerskirch et al. 2015, 2020). Interestingly,  
436 immature appear to have this peak in time spent on the water in spring, suggesting different timing of  
437 moult.

438

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

Stage <sup>1</sup>	Definition	Age <sup>1</sup>	Tracking duration	Behaviour
Juvenile	Following chick fledging in January	1 <sup>st</sup> 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	Nonbreeding 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

440 <sup>1</sup> Stage/Age at which the individuals were equipped with loggers in our study

441 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
Immature	2011-2012	18	17	94	13
Adult sabbatical	2006, 2009	11	11	100	10

442

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

444 albatross

445

	Juvenile <sup>1</sup>		Juvenile <sup>2</sup>		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

446 <sup>1</sup> calculated during 28 months following departure; <sup>2</sup> calculated during 9 months following departure

447 **FIGURES**

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

451

452 Figure 2 Daily flying bouts duration (dry bouts in hours) depending on stage (juveniles, immatures and  
453 adults) and on sex (females and males) for every month since departure from the colony (upper panel)  
454 and for each month of the year (lower panel). Error bars represent  $\pm 1$  sd.

455

456 Figure 3 Daily flying bouts number (dry bouts) for every month since departure from the colony for  
457 juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent  
458  $\pm 1$  s.d.

459

460 Figure 4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures  
461 and adults) and on sex (females and males) for every month since departure of the colony (upper panel)  
462 and for each month of the year (lower panel). Error bars represent  $\pm 1$  sd.

463

464 Figure 5 Daily wet bouts number (bouts on water) for every month since departure from the colony for  
465 juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent  
466  $\pm 1$  sd.

467

468 Figure 6 Daily proportions of time spent on water for every month since departure of the colony for  
469 juveniles-during the first 28 months spent at sea (after departure)- , immatures and adults (upper panel)

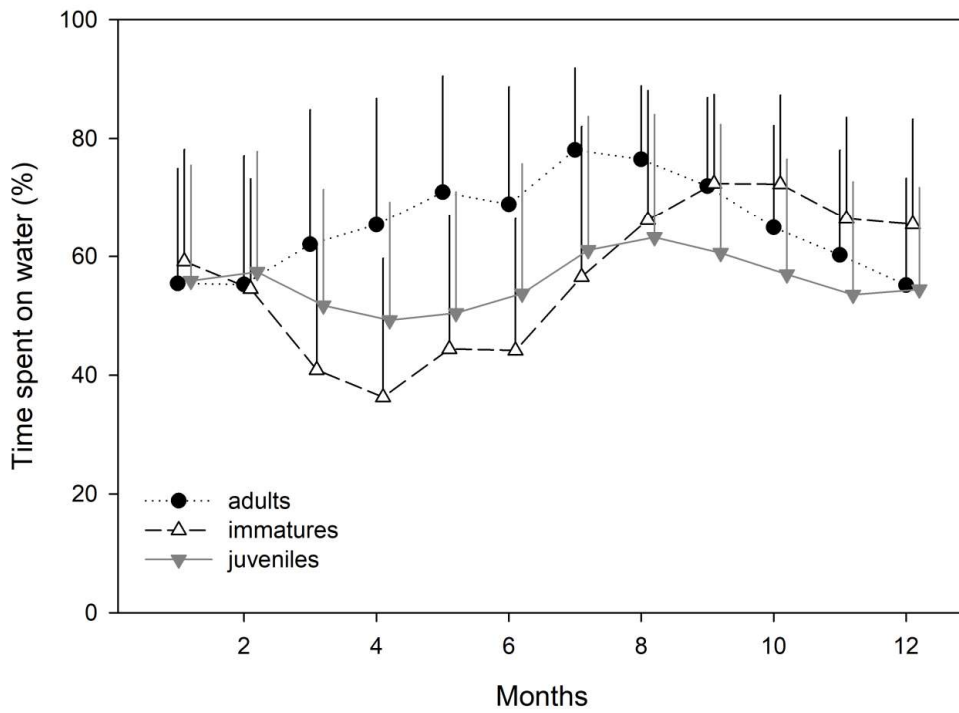
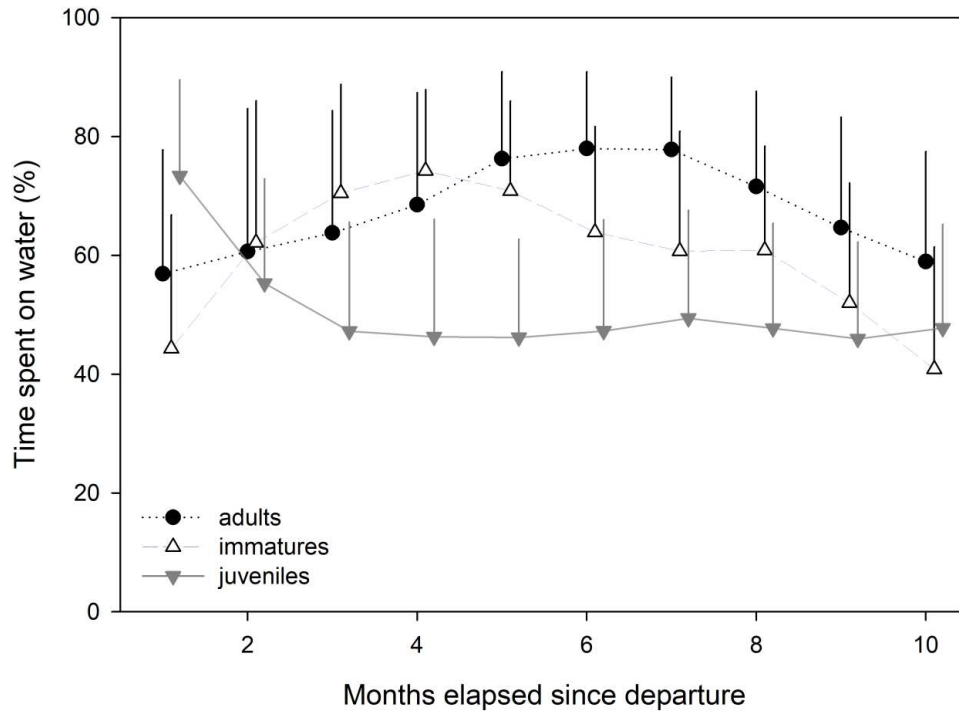


470 and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error

471 bars represent  $\pm 1$  sd.

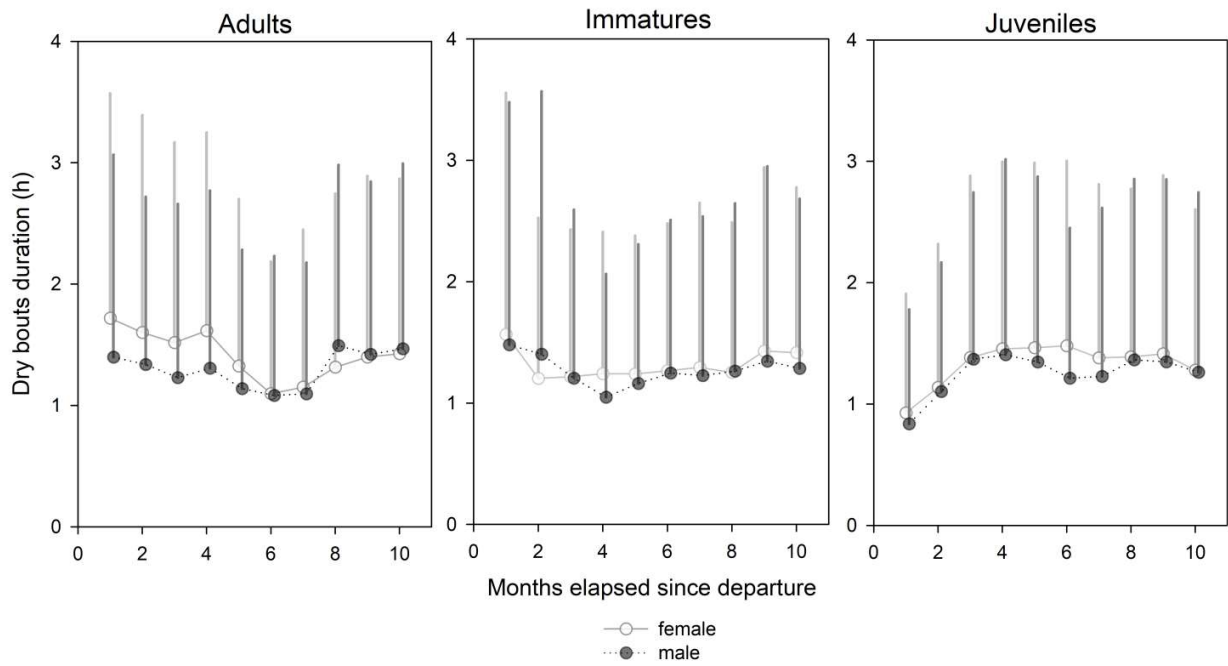
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473 Figure 1



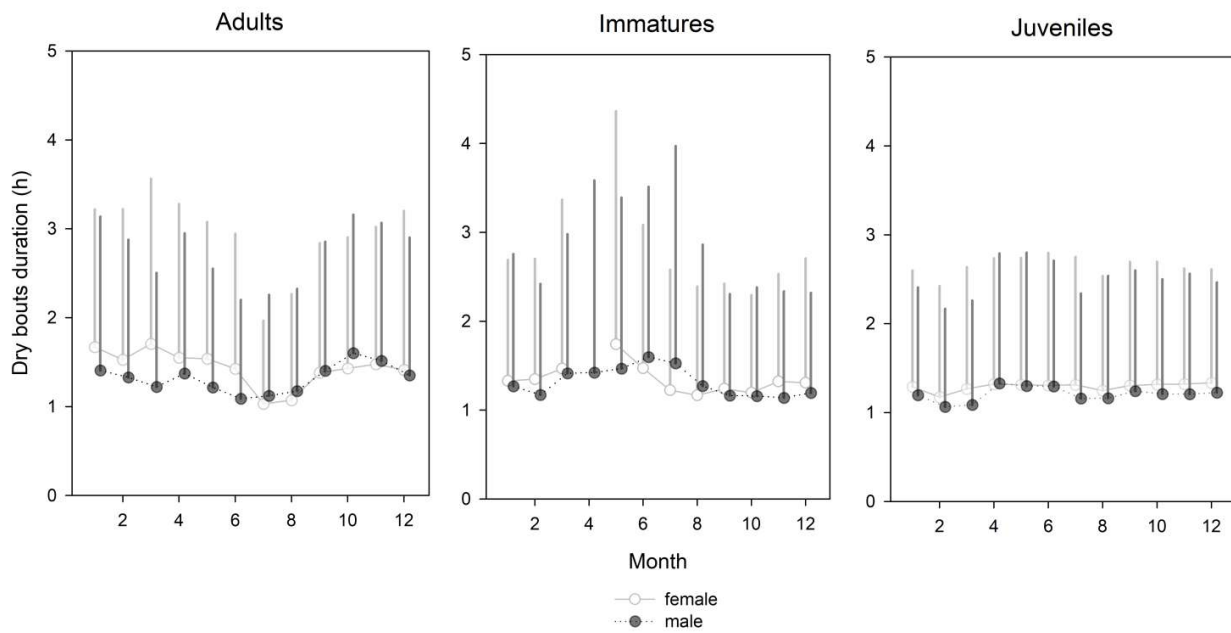
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475 Figure 2



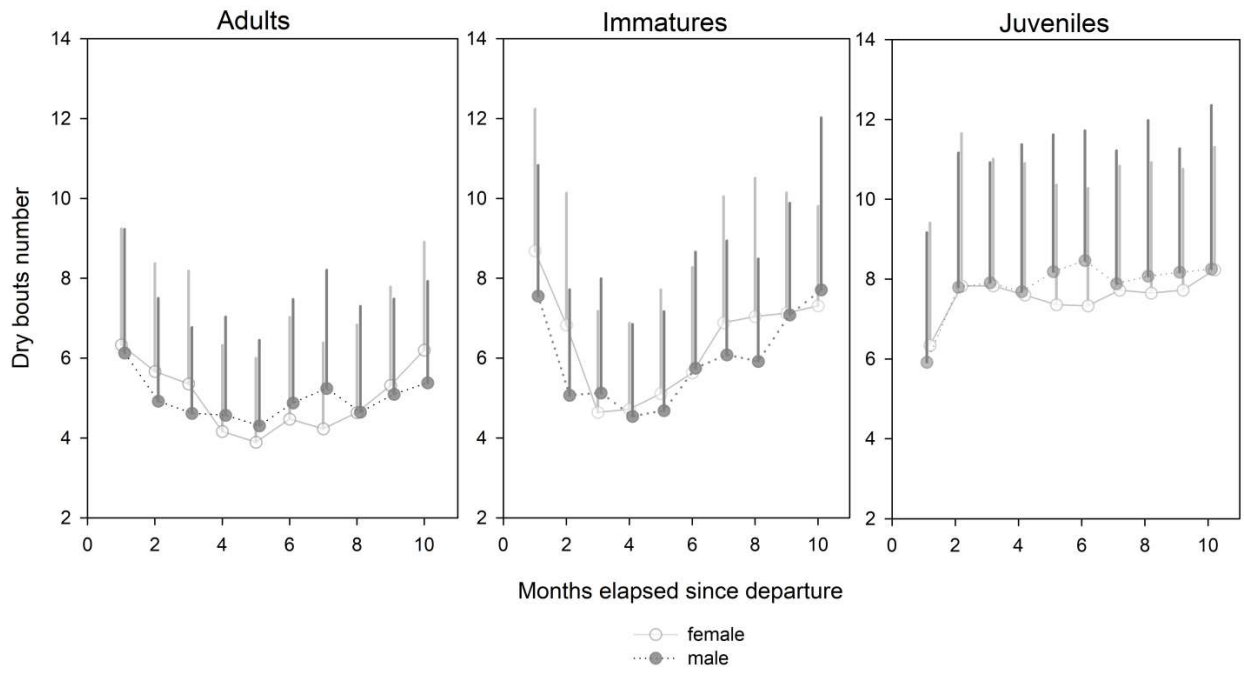
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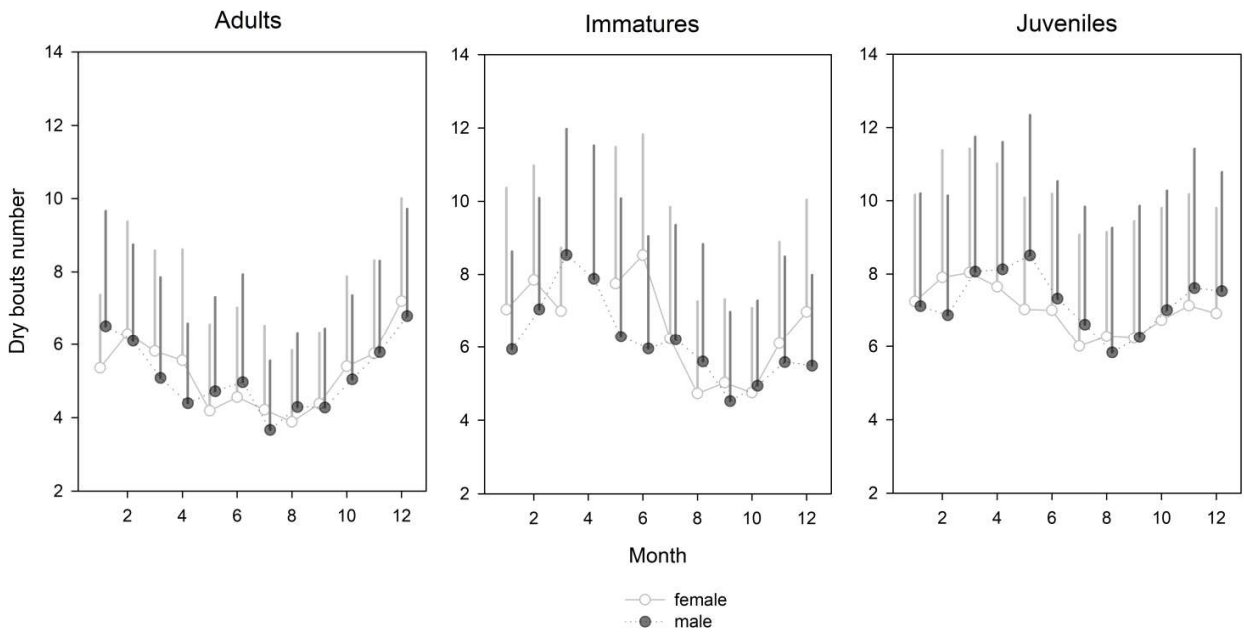
478

479 Figure 3



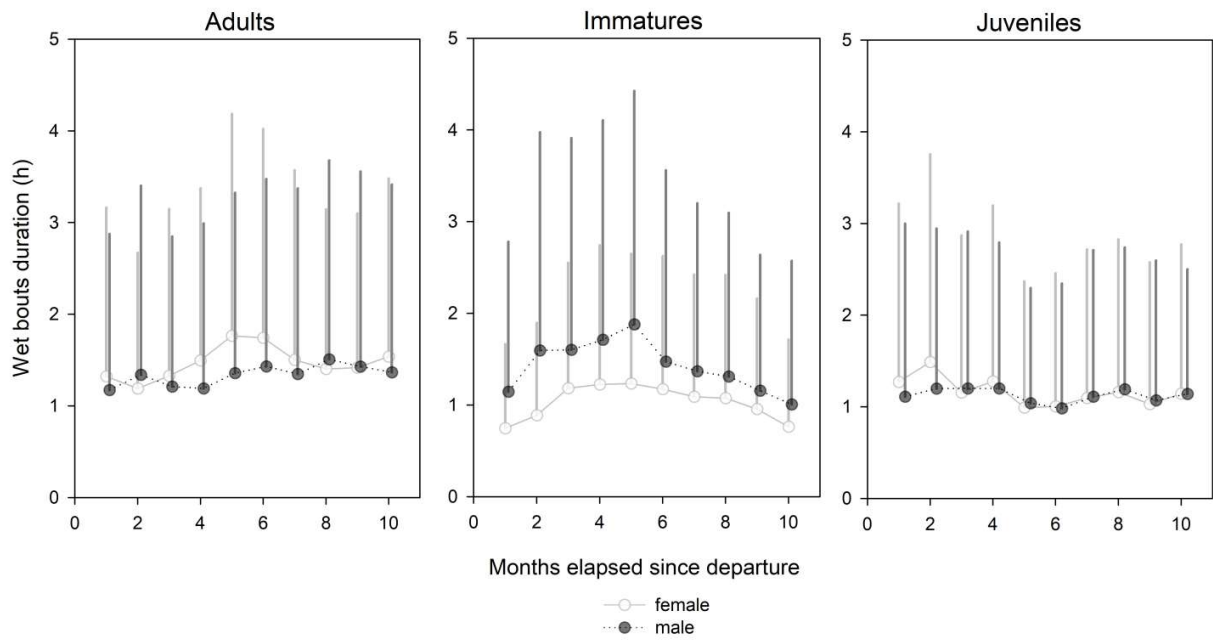
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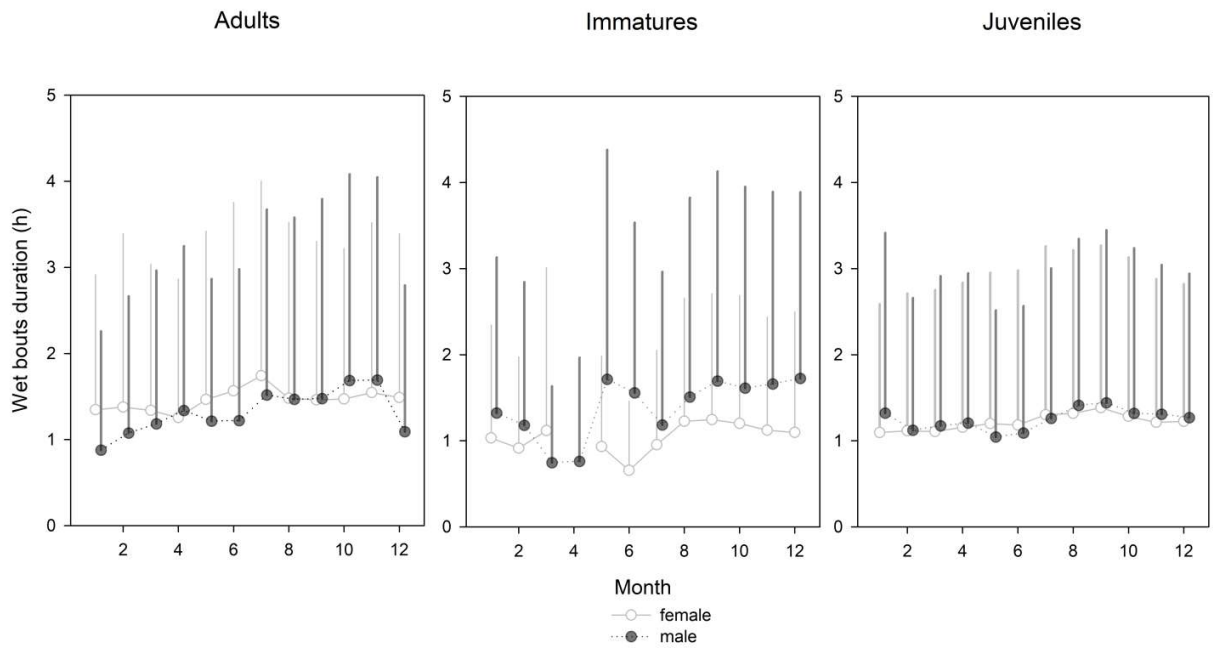


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483 Figure 4

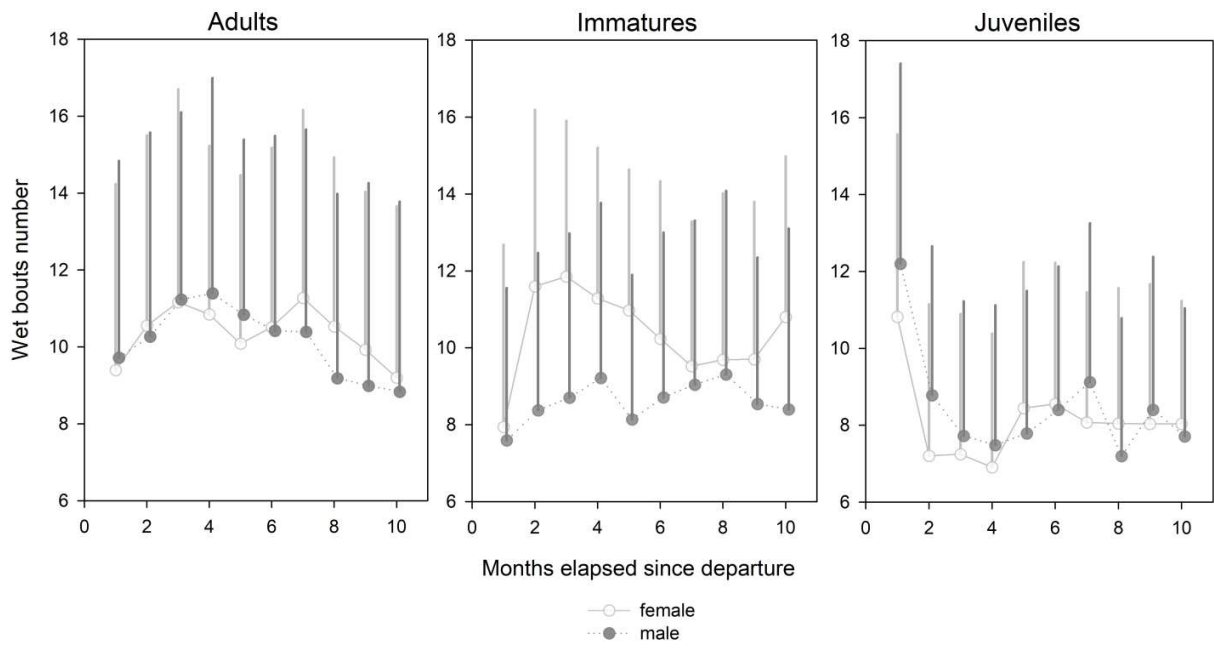


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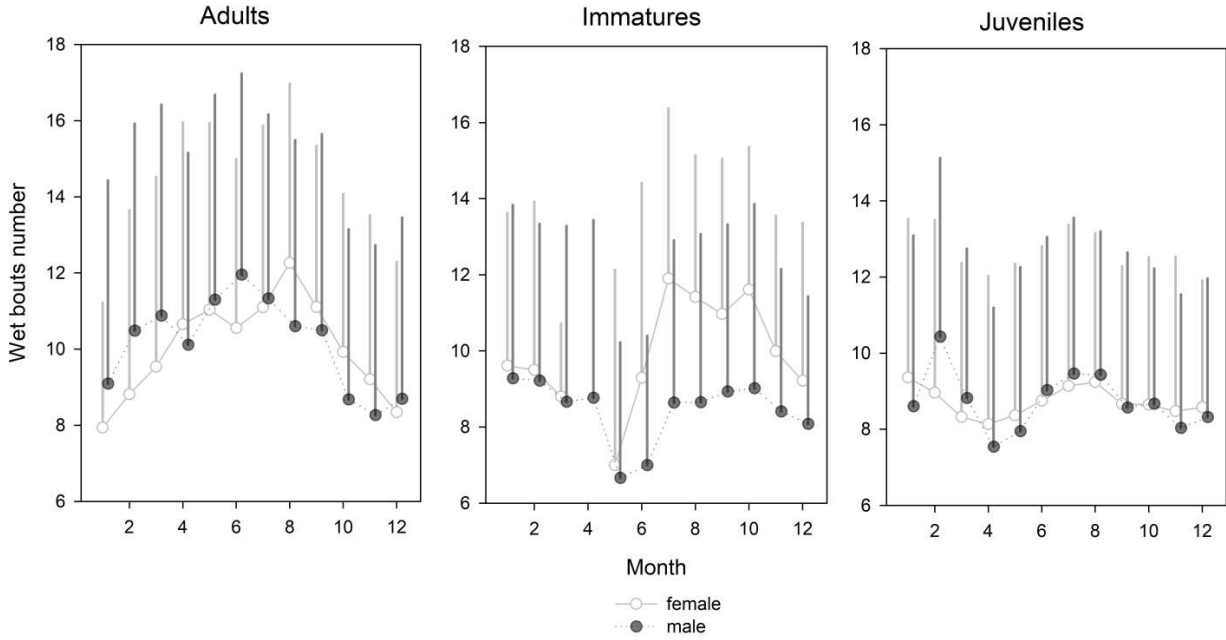
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486 Figure 5



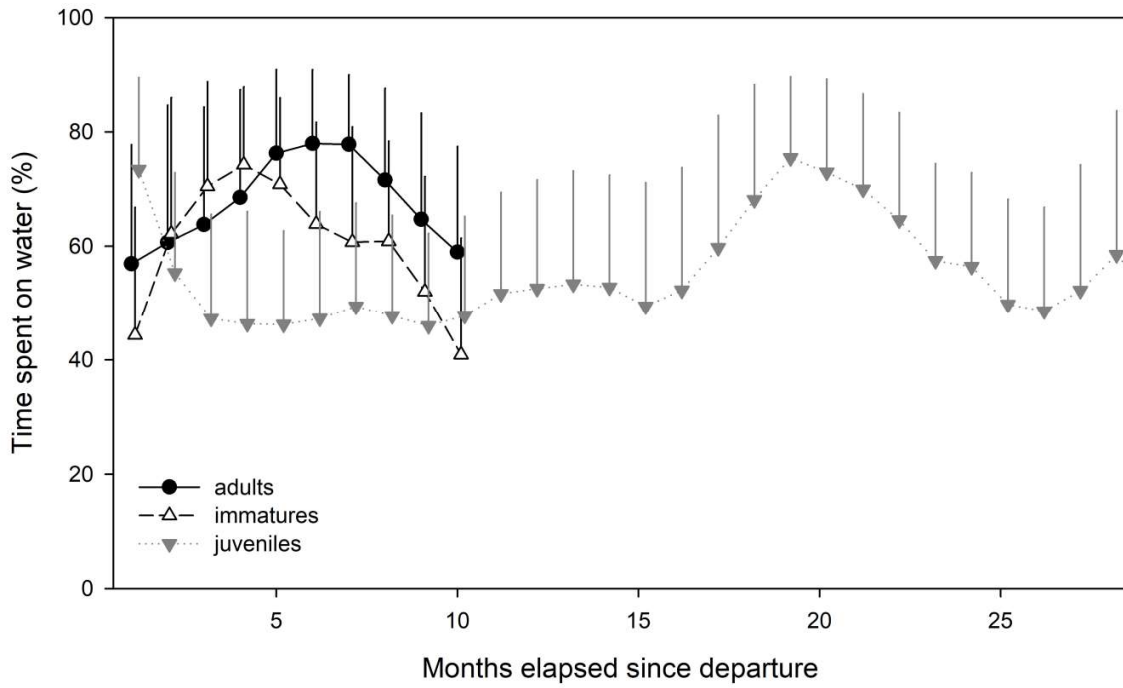
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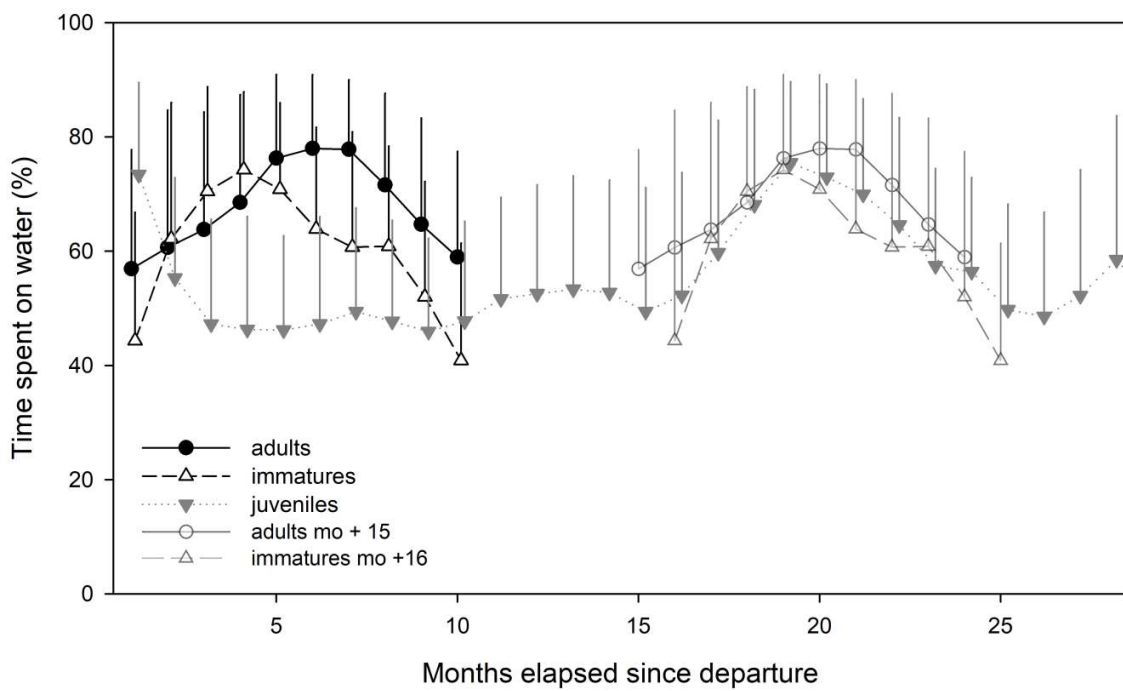
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490 Figure 6



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492



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