TITLE

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

KARINE DELORD[1]*, HENRI WEIMERSKIRCH[1], CHRISTOPHE BARBRAUD[1]

[1] Centre d'Etudes Biologiques de Chizé UMR 7372, CNRS, F-79360 Villiers en Bois, France

Abstract

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

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

Introduction

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

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

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

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

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

In this study, we benefited from a unique dataset of different life stages (juveniles, immatures and adults) and a remarkable duration (up to 28 months for juveniles) to characterise and compare the changes in behaviour at sea when birds leave the colony (for several months: immatures and adults, or years: juveniles before returning to land). We analyse the foraging behaviour, through activity patterns,

of naïve juveniles (first years of independence at sea), immatures (individuals that never bred, age 2-10 years) and adults (individuals that bred at least once, age 8-28 years) of Amsterdam albatross (Table 1). By using miniaturized activity loggers (Global Location Sensing; GLS) to infer foraging behaviour (activity) throughout the successive life stages we addressed the following questions: i) do individuals belonging to different life-stages behave differently? ii) are there detectable progressive changes in activity patterns? It is noteworthy that the loggers used do not yet allow to have longitudinal data (maximum 2-3 years of recorded data) and to cover the entire period until an individual is recruited into the population as a breeding adult, i.e. at least 8 years.

Previous knowledge of the ecology of large albatrosses and Amsterdam albatross described above provides a practical framework for testing predictions about variability in foraging behaviour associated with stage, time elapsed since departure from the colony, seasons and sex which are summarised in Table 2. Given the overlap of spatial distribution between life-stages (not presented here but see Thiebot et al. 2014; de Grissac et al. 2016; Pajot et al. 2021) we predicted that juveniles would compensate for any lack of foraging proficiency by increasing foraging effort and time (i.e. lower time spent on water and longer flying bouts, in other words decreasing time sitting on water and increasing number and duration of flight bouts; Hypothesis (A), Table 2). We also predicted changes in activity of juveniles early in post-fledging followed by more progressive changes. Based on results found on wandering albatross fledglings (Riotte-Lambert and Weimerskirch 2013; Pajot et al. 2021) showing that juveniles reached some adult foraging performances in less than two months, we predicted that changes should be detected in activity parameters early after the juvenile left the colony (within few first months). Overall, juveniles should show contrasted foraging effort (i.e. longer time spent on water, shorter flying effort with fewer and shorter flying bouts) early in post-fledging compared to other life-stages. Due to seasonal changes in food availability individuals will face at sea after leaving the colony and the alleviation of energetic constraints linked to reproduction (for breeding adults) or to alternate

foraging trips at sea and period on land for pair bonding and mating display (for immature birds), we predicted that adjustments of activity will occur according to the time spent (i.e. in months elapsed) since the departure from the colony (Hypothesis (B), Table 2). In juveniles, we predicted early and rapid changes during post-fledging and then more progressive changes. The two hypotheses (A & B) are not mutually exclusive. While our main objective was to study post-fledging foraging behaviour activity as described above, we also accounted for other sources of changes in foraging behaviour. These included temporal (i.e. related to the month of the year) changes in activity parameters for all life-stages due to (i) environmental changes occurring throughout the seasons, to (ii) partial moulting which is suspected to occur outside the breeding period and to (iii) result in reduced activity for adults and immatures (i.e. more time spent on the water; Weimerskirch et al. 2015, 2020), or to sex differences in flight performances (Shaffer et al. 2001; Riotte-Lambert and Weimerskirch 2013; Clay et al. 2020) .

Materials and methods

Study species and data loggers

Amsterdam Island (37° 50’ S; 77° 33’ E) is located in the subtropical part of the southern Indian Ocean. The Amsterdam albatross, like other great albatrosses, is a biennial breeder (Roux et al. 1983; Jouventin et al. 1989), with high survival during juvenile, immature and adult phase (Rivalan et al. 2010). The adults that raised a chick successfully do not start a new breeding cycle after chick fledging, but remain at sea for a sabbatical period (~1 yr; Table 1; Rivalan et al. 2010). However, early failed breeders may start to breed the following year (Rivalan et al. 2010). Immature birds may visit the colony when they are 4–7 yrs old, but generally only start breeding at 9 yrs old (Table 1; Weimerskirch et al. 1997a). Juvenile birds fledge and migrate independently from the adults in January (Table 1). Exact fledging dates were not known for juveniles but were assessed from activity pattern as juvenile birds land on water quickly after leaving the colony (Weimerskirch et al. 2006). Amsterdam albatrosses were

133 monitored annually since 1983 and all individuals were individually marked (numbered stainless steel
134 and plastic engraved colour bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age
135 (79 individuals since the beginning of the study) and chicks of the year were banded, weighed (body
136 mass ± 50 g using a Pesola® spring balance) and measured (wing length ± 1 mm with a ruler, tarsus
137 length, bill length, and bill depth ± 0.1 mm with calipers).
138 In Amsterdam Island oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical
139 from the colder sub-Antarctic waters (Belkin & Gordon 1996). Though the diet and foraging strategy of
140 Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour
141 compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021;
142 see Supplementary for species biological aspects). The wandering albatross is known to forage over
143 extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008) referred as
144 '*foraging-in-flight*', the lowest energy consuming feeding strategy. However, the strategy tends to
145 change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014), and could result in more
146 frequent and shorter bouts on the water in a '*sit and wait*' technique.

147

148 Thiebot et al. (2014) showed that adult Amsterdam albatrosses during their post-breeding sabbatical
149 period moved widely (31° to 115° E), mostly exhibiting westwards wider-scale migratory movements
150 (*sensu* Weimerskirch et al. 2015a) reaching >4000 km from the colony exploiting continuously warm
151 waters (~18°C; see Supplementary). The immature birds moved widely in longitude (0° to 135° E),
152 exploiting exclusively warm waters 17°-18° C. Juveniles exhibited very large migratory capacities over
153 the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large
154 range of latitudinal gradient (27° to 47° S). De Grissac et al. (2016) compared trajectories (i.e. departure
155 direction or orientation toward specific areas) of juveniles and adults and showed that juveniles

156 performed an initial rapid movement taking all individuals away from the vicinity of their native colony,
157 and secondly performed large-scale movements similar to those of adults during the sabbatical period.
158 GLS are archival light-recording loggers used to study activity of birds over periods lasting up to ~ 2
159 years. GLSs record the ambient light level every 10 min, from which local sunrise and sunset hours can
160 be inferred to estimate location every 12 h (Wilson et al. 1992). GLS also recorded saltwater immersion
161 data by testing for saltwater immersion at regular interval, storing the number of samples wet (>0) at
162 the end of each 10 min period. We used saltwater immersion to estimate daily activity budget. Despite
163 the higher mean spatial error of location estimates with these devices (over 100 km; Phillips et al.
164 (2004a)), GLS loggers allowed us to track the birds for prolonged periods with minimal disturbance to
165 them. We considered the following stages with respect to the ages when GLS were deployed (see Table
166 1): juvenile, as a fledgling equipped with a GLS just before leaving the colony for the first time;
167 immature, as a non-breeding young bird that had never bred equipped with a GLS when visiting the
168 colony; adult, as a breeding adult equipped with a GLS during the incubation or brooding period which
169 successfully fledged a chick and thereafter took a sabbatical year. To date, we have retrieved 40 of the
170 50 GLS loggers deployed in total over 4 years, from which 33 individual tracks were estimated (Table 1).
171 Our original aim was to collect activity data on the three stages over a long period of time (>1 year).
172 These data are available from a total of 10 adults tracked throughout their sabbatical period, 13
173 immature birds and 10 juvenile birds (up to 3.2 years).
174
175 **Data processing**
176 The raw immersion data were values from 0 (no immersion or dry, in flight or sitting on the ground) to
177 200 (permanently immersed in sea water or wet, indicating the number of 3 s periods during 10 min
178 blocks when the sensor was immersed in saltwater). Loggers recorded the proportion of time in
179 seawater at 10 min intervals, which we summarized as hours in the water per day (hereafter time spent

on water; 10 min blocks immersion data > 0). This measure is a reliable proxy of foraging effort linked to foraging behaviour of the species which enters the water principally to forage (Weimerskirch and Guionnet 2002). Additionally, the duration of the bouts spent entirely immersed (10 min blocks immersion data = 200) was calculated daily (hereafter referred as wet bouts duration). Conversely, when birds are not on land, the time spent dry was interpreted as flying (and thus not feeding). The duration of the bouts spent entirely dry (10 min blocks immersion data = 0) was calculated daily (hereafter referred as dry bouts duration). Additionally the numbers of bouts (number of wet bouts - sitting on water-and of dry bouts -flying) were obtained daily. Although the loggers integrated activity within each 10 min block and so did not provide the exact timing of landings and take-offs, Phalan et al. (2007) found for comparative purposes that bouts defined as a continuous sequence of 0 values for flight (dry) and a sequence of values of 1 or greater for wet bouts, were suitable proxies for activity.

To select the data corresponding to periods spent at sea after leaving the breeding site, we used the following criteria on activity to define the departure time from the colony for each stage: 1) juveniles, the first bout spent on seawater (wet bouts duration) > 1h based on Argos Platform Transmitters Terminals (PTT) tracking data (data obtained in a other project and not shown here, Weimerskirch et al. unpublished data); 2) immatures and adults, the last bout spent flying (dry bouts duration) > 12h based on PTT tracking data (Weimerskirch et al. unpublished data). Using these criteria we obtained departure months as follows: 1) the juveniles fledged from the colony from January to March, 2) the immatures left between April and August, and 3) the departures of sabbatical adults were spread over two periods, first between December and February and then from May to July.

Statistical analyses

Variation in activity parameters

204 The aim was to determine whether distinct foraging behaviours could be detected across the patterns of
205 variation of wet/dry data, and then to appraise how these behaviours varied over time and among
206 individuals. First, to deal with the fact that wet/dry metrics were interrelated (number of wet bouts
207 sitting on water and time spent on water, wet bouts duration and dry bouts duration, wet bouts number
208 and dry bouts number) and to avoid redundancy, we ran principal components analyses (PCA built with
209 the 'PCA' function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe
210 changes in behaviour over time and stages using gradients of activity we ran PCA for i) all stages (PCS;
211 based on activity data collected during the first ten months post-departure) and for ii) juveniles only, as
212 an additional goal was to determine changes in activity patterns during the first two years of life (PCJ;
213 based on activity data collected during the first twenty-nine months post-departure).
214 Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance.
215 For juveniles, the first three principal components (PCJ) explained 92.2% of the total variance. The
216 detailed results of PCA and the variables retained for each axe are summarised in Table 3.
217
218 Second, we used generalized additive mixed models (GAMMs, built with the 'gam' function, itsadug and
219 mgcv package (Lin and Zhang 1999; Wood 2015)) with the values associated with each of the three first
220 axes of the PCA as the dependent variables. We ran separate models testing for variability in activity
221 parameters i) for all stages combined (PCS) and ii) for juveniles (PCJ), based on different duration of
222 datasets (28 months since departure for juveniles and 9 months since departure for immatures and
223 adults; see Supplementary; Table S1). Thus, for i) we considered the lowest number of months elapsed
224 since departure available (9 months since departure). Months elapsed since departure (the duration
225 elapsed since fledging expressed in month, i.e. the first month after fledging and so on), month of the
226 year (i.e. January and so on), sex, and stage (only for i)) were included as fixed effects. The interactions
227 between stage and time were included as fixed effects to test for the prediction that differences should

228 vanish with time passed since fledging. To test for the importance of individual variability in our results
229 we built models with or without random effects. We compared models without random effect, models
230 with random intercepts, and models with random slopes and intercepts to test whether the rate of
231 change of activity parameters as a function of time elapsed since departure varied between individuals
232 (Zuur 2009a). Models included month elapsed since departure as a continuous covariate modelled with
233 non-parametric smoothing functions (Wood 2017). We limited the amount of smoothing (k) with the
234 'gam.check' function following Wood (2017) for each spline to avoid excessive flexibility and model
235 overfitting that would have no ecological meaning. Models including all combinations of explanatory
236 variables and random effects were then tested and ranked using their Akaike Information Criterion (AIC)
237 values and Akaike weights following the Information-Theoretic Approach (Burnham and Anderson
238 2002). The model with the lowest AIC was considered as the best model. Two models separated by a
239 difference in AIC values of less than 2 were assumed to fit the data similarly.
240
241 Although sexes and stages differed for some body size measurements (see details in Supplementary), we
242 could not include body size as an additional explanatory variable in GAMMs testing for factors of
243 variation in activity patterns due to small sample sizes in each sex and stage category (see Table 1).
244 Spatial and statistical analyses were performed using R (R Core Team 2021). Values are means ± SD.
245
246 **Results**
247 The most parsimonious models explaining variations in activity parameters in the Amsterdam albatross
248 included time elapsed since departure from the colony, month of the year, stages and sexes (Tables 4
249 and 5; Supplementary Figures S1 - S5; Tables S1), whatever the synthetic activity variables considered
250 (PC1S, PC2S and PC3S; Table 4). The interaction between stage and time elapsed was significant for the
251 first synthetic activity variable (PC1S). Selected models also included random effects on intercepts and

slopes, indicating inter-individual variability in activity and inter-individual variability in the rate of change of activity as a function of time elapsed since departure from the colony.

In juvenile Amsterdam albatrosses, the most parsimonious models explaining variations in activity included time elapsed since departure from the colony, month of the year for all three activity variables considered (Table 5 and 6; PC1J, PC2J and PC3J), and sex was retained only for two variables (PC2J and PC3J). Selected models also included random effects on intercepts and slopes, indicating inter-individual variability in activity and variability in the rate of change of activity as a function of time elapsed since departure from the colony (Supplementary Figures S6).

Changes in activity for all stages

The two synthetic activity variables (PC1S, PC2S) varied significantly with time exhibiting clear nonlinear temporal patterns (Figure 1). These variations were related to the time elapsed since their departure from the colony and showed seasonal changes (indicated by the month of the year; Supplementary Figures S1 - S5; Tables S1 and S2). With increasing time since departure, birds spent lower percentage of time on water and made shorter wet bouts. They spent less percentage of time on water during the period March to July compared to rest of the year (PC1S, Supplementary Figures S1 - S5). They made longer and fewer bouts on water during the period April to November, and shorter flying bouts during the period November to February. Juveniles showed strong temporal changes in activity linked to the time elapsed since departure from the colony in the first two months after fledging (Supplementary, Figure 2). In immatures and adults the temporal pattern appeared reversed compared to juveniles (Supplementary, Figure 2).

Compared to adults, immatures and even more so juveniles, spent a lower percentage of time on water (Table 5, Supplementary Figures S1) and made more flying bouts (PC1S; Supplementary Figures S2), made shorter and fewer bouts on water (PC2S; Supplementary Figures S4-S5), and made longer flying

bouts (PC3S; Supplementary Figures S2). Males spent a higher percentage of time on water and made fewer flying bouts (PC1S), longer and more numerous bouts on water (PC2S) and shorter flying bouts (PC3S) compared to females.

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

PC1J and PC2J varied significantly with time exhibiting clear nonlinear temporal patterns (Figure 3; Supplementary Figures S7 - S11; Tables S1 and S3a, 3b). Juveniles seemed to alternate periods of lower percentage of time spent on water combined with more numerous flying bouts (April) with periods of higher percentage of time on water combined with fewer flying bouts (February, July-October; PC1J, not illustrated). The seasonal change was also observed through longer and fewer bouts spent on water and shorter flying bouts at the end of the year (PC2J: September-December). Juveniles, during the first 28 months after fledging, increased the time spent on water while decreasing the number of flying bouts (Figure 3a).

PC2J and PC3J varied significantly with sex (Supplementary Figures S7 - S10; Tables S5b, 5c), indicating that juvenile males made shorter and more numerous bouts on water (PC2J) and shorter flying bouts (PC3J) compared to females (Supplementary Figures S7 - S10; Tables S5b, 5c).

Discussion

In this study, we benefited from a unique comprehensive dataset of remarkable duration (up to 28 months) to characterise the post-fledging behaviour of naïve seabirds. Using miniaturized activity loggers (GLS), we showed clear differences and changes in activity characteristics depending on life-stages. By comparing changes in behaviour at sea and foraging parameters of juveniles after their departure at sea with those of immatures and adults in the Amsterdam albatross, we showed that

juveniles differed from immatures and adults in their activity values and patterns. Activity also varied according to time and sex. Our study allows us to compare foraging behaviour among life stages in a long-lived endangered seabird species, while also providing new insights into the development of foraging patterns in naïve individuals over a multi-year period.

Stage specific changes

The birds were found to behave differently according to their stage whatever the activity variables considered, indicating differences in foraging behaviour. Overall, juveniles spent lower percentage of time on water compared to immatures and adults. During the first months following their departure from the colony the proportion of time spent on water by immatures and adults showed a dome-shaped curve peaking three to five months after departure. During the same period of time, the proportion of time spent on water by the juveniles changed strongly, with values dropping off in the first two months and then remaining low and overall lower than in adults and immatures. This might indicate a lower foraging activity in naïve birds. During the same period, the duration and number of water bouts also exhibited progressive change. These patterns suggest an early and gradual change in foraging behaviour so that juveniles progressively could behaved similarly to immatures and adults (reaching similar values in activity covariates). This suggest a progressive behavioural change in movements during the first two months after fledging. It is noteworthy that the multi-monthly bell-shaped pattern observed during the first 10 months after departure in immatures and adults appears to be mirrored in juveniles 15-16 months later (see Figure S11). Despite such possible similarities (% time spent on water), there are still some differences between stages (see Supplementary). Since % time spent on water partly reflects foraging, this seems to indicate that juvenile individuals may have weaker foraging skills during their first two months at sea. Although behavioural changes can often equate to improved performance (e.g. Campioni et al. 2020) this is not always the case. The emergence of juvenile birds as more '*adult like*' in

324 their foraging/flight behavioural patterns is not necessarily a sign of improvement. For example, it could
325 be partly due to individual differences in area use with different environmental conditions encountered
326 (food abundance, wind regimes).
327 Since all stages of the Amsterdam albatross forage in the same water masses (see Thiebot et al. 2014),
328 differences in foraging behaviour were presumably not due to different oceanographic characteristics as
329 observed in other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al. 2020b). These
330 differences could be due to a combination of lack of experience, poor knowledge of the environment,
331 use of distinct cues and/or physical immaturity leading to sub-optimal behaviour (Shaffer et al. 2001;
332 Frankish et al. 2020a, 2022). It is likely that increasing exposure to diverse foraging situations allows
333 juveniles to rapidly accumulate foraging experience and improve various aspects of foraging.
334 Results suggest that immatures may differ from both adults and juveniles in some aspects of their
335 behaviour. While most of the activity parameters and the temporal patterns showed similarities with
336 adults when considering the time elapsed since departure, they seemed rather comparable to juveniles
337 when considering seasonal aspects (month of the year). Such differences can be explained by several
338 non-exclusive explanations: i) similar management of energy constraints than adults, as post-breeding
339 adults and immatures are less constrained in their central-place foraging strategies (Campioni et al.
340 2016), ii) comparable capacity to respond to local resource availability in their foraging behaviour than
341 juveniles (Frankish et al. 2022), and iii) incomplete acquisition of more long-term learning of complex
342 movement strategies (Thorup et al. 2003; Votier et al. 2011; Rotics et al. 2016). Disentangling these
343 hypotheses can be achieved by combining higher resolution movement data with longer longitudinal
344 studies covering all three life stages for the same individuals.
345
346 What might be designated as '*lower performance*' of juveniles found in our study is consistent with
347 studies on wandering albatrosses and Amsterdam albatrosses (Riotte-Lambert and Weimerskirch 2013;

348 de Grissac et al. 2017; Pajot et al. 2021) during the first weeks at sea Juvenile albatrosses behaved
349 differently in first month after fledging (i.e. speed and sinuosity of movements) and readily use similar
350 foraging strategies as adults (Frankish et al. 2022). Additional skills (such as detection of prey at the
351 surface, detection of other foraging seabirds, navigational skills…) need to be acquired during the
352 immature period before the efficiency of these behaviours matches that of adults. This is also typical of
353 other seabird taxa, which show progressive improvement in flight performance with the numbers of
354 days since fledging (Yoda et al. 2004; Mendez et al. 2017; Collet et al. 2020; Corbeau et al. 2020;
355 Frankish et al. 2022). For example juvenile brown boobies *Anous stolidus* improved their flight abilities
356 (Yoda et al. 2004). In contrast, flight capability (flight speed and sinuosity) comparable to that of adults
357 allows juvenile white-chinned petrels *Procellaria aequinoctialis* to rapidly fly over long distances away
358 from the colony (Frankish et al. 2020).
359 The progressive change of movement behaviours (foraging parameters estimated from activity
360 parameters improved with time elapsed) quantified in juvenile Amsterdam albatrosses, could be either
361 due to physical development and/or experience gain. Elucidating the mechanisms of the transition to
362 independence in early life stages is however crucial for understanding the causes of higher juvenile
363 mortality in long-lived species (Fay et al. 2015; Payo-Payo et al. 2016).
364
365 *Temporal changes and sex differences in activity*
366 The temporal variability of activity was found whatever the life-stage considered. Part of the activity
367 changes observed following the departure of juvenile Amsterdam albatrosses may illustrate the swift
368 change in travel and movement behaviour, reflecting a more '*adult-like*' behaviour, not indicating
369 necessarily an improvement of flight performances and of the ability to cope with changing (i.e.
370 increasing wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such as
371 albatrosses. Both extrinsic (i.e. environmental conditions) and intrinsic (i.e. energetic demands linked to

372 plumage moult) factors could be involved in the modulation of foraging behaviour, which can be
373 reflected in the temporal variability.
374 Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996;
375 Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in
376 both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). Stage-specific
377 and sex-specific differences in moult extent occur in wandering albatross, suggesting important
378 constraints (Weimerskirch 1991; see Supplementary). Adult birds during the non-breeding season
379 appear to spend much more time on the water during winter, suggesting that partial moult may occur at
380 this time (Weimerskirch et al. 2015b, 2020). Interestingly, immature individuals appear to have a similar
381 peak in time spent on the water in spring, suggesting different timing of moult.
382 Consistently, we found that males flew for longer periods (dry bouts duration) compared to females.
383 When considering all stages, males spent a higher percentage of time on water compared to females.
384 Males in all stages did more bouts on water and juvenile males shorter wet bouts, compared to females.
385 Contrary to the wandering albatross (Weimerskirch et al. 2014), male and female Amsterdam
386 albatrosses forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger
387 et al. 2013; Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were
388 caused by differences in foraging habitats. Sex-specific behavioural differences are common in sexually
389 dimorphic seabirds as reviewed in Wearmouth and Sims (2008), where the smaller sex usually
390 undertakes longer trips. Sexual size dimorphism can result in differences in aerial agility, foraging area
391 and behaviour, and provisioning rate and preferred prey (Gonzales-Solis et al. 2000; Phillips et al. 2004b,
392 2011; Weimerskirch et al. 2009; Austin et al. 2019; Barbraud et al. 2021). It has also been suggested that
393 size matters probably because the smaller and lighter sex has a higher foraging and flight efficiency
394 (Shaffer et al. 2001; Clay et al. 2020), suggesting that lighter and lower wing loaded female wandering
395 albatrosses, compared to males, are probably better able to exploit subtropical and tropical waters

where winds are lighter. Following this, it can be hypothesized that female Amsterdam albatrosses have a greater advantage in foraging in the subtropical environment than males. Sex differences in the acquisition of foraging performance during the first months after fledging yet remain to be explored.

Individual variability in activity

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

Conclusion

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

420 fewer flying bouts). Patterns of activity parameters in juveniles after independence suggested a
421 progressive change of foraging performances during the first two months after fledging. Regardless of
422 life stage considered, activity parameters exhibited temporal variability reflecting the modulation of
423 foraging behaviour presumably linked to both extrinsic (i.e. environmental conditions such as variability
424 in food resources or in wind) and intrinsic (i.e. energetic demands linked to plumage renew during
425 moult) factors. Sex differences in activity parameters according to time since departure from the colony
426 and season were consistent with the sexual dimorphism in the Amsterdam albatross. Overall, an
427 expected change in behaviour, resulting from the experience gained, may reflect an improvement in
428 skills occurring during a period of learning through the immaturity phase which still would need to be
429 confirmed by directly assessing foraging performance. Results from our study suggest that the lower
430 foraging activity of juvenile Amsterdam albatrosses may partly explain their lower survival compared to
431 adults. However, despite foraging metrics of juveniles investigated here reached values observed for
432 adults quite rapidly, immature survival remains lower than adult survival during several years (Rivalan et
433 al. 2010). Therefore, more detailed information such as foraging performance realized (the amount or
434 quality of preys obtained by juveniles) or energetic expenditure are needed to better understand age-
435 specific differences in life history traits such as survival and the dynamics of the species.

436

Ethics

All work was carried out was approved by the French Polar Institute (IPEV) ethics committee.

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This study is a contribution to the National Plan of Actions for Amsterdam albatross.

Authors contribution

K.D. and C.B. conceived the study. H.W. secured funding. K.D. prepared and analysed the data. C.B. provided feedback on the analyses. K.D. wrote the first draft and all authors contributed to editing versions of the manuscript.

457 Table 1 Chronological characteristics of life-cycle stages (adapted from Thiebot et al. 2014) and sample sizes of birds tracked using Global

458 Location Sensing (GLS) of Amsterdam albatross

Stage[1]	Definition	Age[1]	Tracking duration	Behaviour	Years of deployment	Deployed (n)	Recovered (n)	Recovery rate (%)	GLS with data (n)
Juvenile	Following chick fledging in January	1st year	~2.5 years	Chicks disperse at sea after leaving the colony for the first time	2011	21	12	57 (*t*+9)	10 (4 F - 6 M)[2]
Immature	After juvenile movements, until first breeding attempt (at an average age of 9 years old)	~2-10 years	~1 year	Non-breeding young birds forage at sea and occasionally visit the colony for mating	2011-2012	18	17	94	13 (3 F - 9 M – 1 NK)
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	2006, 2009	11	11	100	10 (6 F - 4 M)

459 [1] Stage/Age at which the individuals were equipped with loggers in our study; [2] number of females F and males M, or not known NK for each stage

460 Table 2 Hypotheses and predictions about the factors driving differences in activity (time spent on water, number and duration of

461 flying bouts, number and duration of water bouts) year-round in Amsterdam albatrosses. The two hypotheses are not mutually

462 exclusive.

	Predictions		
Hypothesis	(1) Time spent on water (%)	(2) Flying bouts (number/duration)	(3) Water bouts (number/duration)
(A) Age and stage specific	Juveniles: increased foraging time/effort and thus lower time spent on water (1), longer flying bouts (2) and shorter water bouts (3) than other stages		
(B) Temporal changes - internal requirements: moult/energetic effects	Adults/immatures: two-periods pattern including one with lowering activity Juveniles: change in foraging skills corresponding to gradual change with less time sitting on water (lower time spent on water (1)), increasing flying bouts duration and number (2) and decreasing water bouts duration and number (3), during the 1st month after fledging Adjustment in foraging effort to energetic requirements or moult constraints according to time elapsed since departure: higher time spent on water (1), lower flying bouts duration and number (2) and higher water bouts duration and number (3) during moulting		

463 Table 3 Results of principal components analyses (PCA) on six wet/dry metrics on Amsterdam albatross

Life-stages	Principal components	Total variance explained (%)	Time spent on water	Dry bouts duration	Dry bouts number	Wet bouts duration	Wet bouts number
All	First (PC1S)	41.5	+ (r = 0.97)[1]		- (r = -0.79)		
	Second (PC2S)	32.5				+ (r = 0.79)	- (r = -0.75)
	Third (PC3S)	20.2		+ (r = 0.74)	- (r = -0.44)		
Juveniles	First (PC1J)	42.3	+ (r = 0.98)		- (r = -0.76)		
	Second (PC2J)	32.2				+ (r = 0.72)	- (r = -0.75)
	Third (PC3J)	20.7		+ (r = 0.48)	- (r = -0.46)	- (r = -0.46)	

464 [1] the symbol used gives the sign of the correlation (+: positive, -: negative); the number in brackets indicates the value of the correlation
465 coefficient r

466

467

468 Table 4 Model selection for variation in activity parameters of Amsterdam albatrosses in relation to sex, stage, number of months spent since
469 departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the
470 year (i.e. January and so on)

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1S)				
M_5	Month elapsed + Month + Stage + Sex + Month elapsed: Stage	Month elapsed: Individual	26461.62	
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	27224.79	-763.17
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	27276.18	-814.56
M_2	Month elapsed + Month	Month elapsed: Individual	28322.25	-1860.63
M_1	Month elapsed	Month elapsed: Individual	28591.69	-2130.07
M_0	Null model		28874.42	-2412.80
Bouts spent on water (PC2S)				
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	25751.47	
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	25752.62	-1.15
M_2	Month elapsed + Month	Month elapsed: Individual	25756.37	-4.90
M_1	Month elapsed	Month elapsed: Individual	25803.80	-52.33
M_5	Month elapsed + Month + Stage + Month elapsed: Stage	Month elapsed: Individual	26750.55	-999.08
M_0	Null model		26903.12	-1151.65

Bouts spent dry -flying (PC3S)				
M_4	Month + Stage + Sex	Month elapsed: Individual	22427.29	
M_3	Month	Month elapsed: Individual	22509.79	-8.14
M_2	Month elapsed	Month elapsed: Individual	22539.75	-82.50
M_1	Null model	Month elapsed: Individual	22540.25	-112.96
M_0	Null model		23042.26	-614.97

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

472 Table 5 Values of activity parameters (mean ± sd) recorded using Global Location Sensing (GLS) depending on stage and sex of Amsterdam

473 albatross

474

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

475 [1] calculated during 28 months following departure; [2] calculated during 9 months following departure

476 Table 6 Model selection for variation activity parameters for juvenile Amsterdam albatrosses in relation to sex, number of months spent since
477 departure (month elapsed: duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on) and month of the
478 year (i.e. January and so on)

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1J)				
M_2	Month elapsed + Month	Month elapsed: Individual	21625.69	
M_1	Month elapsed	Month elapsed: Individual	21864.11	-238.42
M_0	Null model		22109.52	-483.83
Bouts spent on water (PC2J)				
M_3	Month elapsed + Month + Sex	Month elapsed: Individual	19999.00	
M_2	Month elapsed + Month	Month elapsed: Individual	20004.65	-5.65
M_1	Month elapsed	Month elapsed: Individual	20072.42	-73.42
M_0	Null model		20417.76	-418.76
Bouts spent dry -flying (PC3J)				
M_3	Month + Sex	Month elapsed: Individual	17541.02	
M_2	Month elapsed	Month elapsed: Individual	17549.00	-7.98
M_1	Null model	Month elapsed: Individual	17548.75	-7.73
M_0	Null model		17708.47	-167.45

479 Models are ranked according to decreasing statistical support, as indicated by AIC. The first best models are show

FIGURES

Figure 1 Modeled a) first and b) second axis of principal components analysis of activity parameters for all stages (e.g. adult, immature and juvenile) of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval. Boxplot represent raw data. The first axis correlated positively with time spent on water and negatively with dry bouts number and the second axis correlated positively with wet bouts duration and negatively with wet bouts number.

Figure 2 Modeled a) first, b) second and c) third axis of principal components analysis of activity parameters for 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 3 Modeled a) first and b) second axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model. Dotted lines indicate 95% confidence interval. Boxplot represent raw data.

Figure 1a

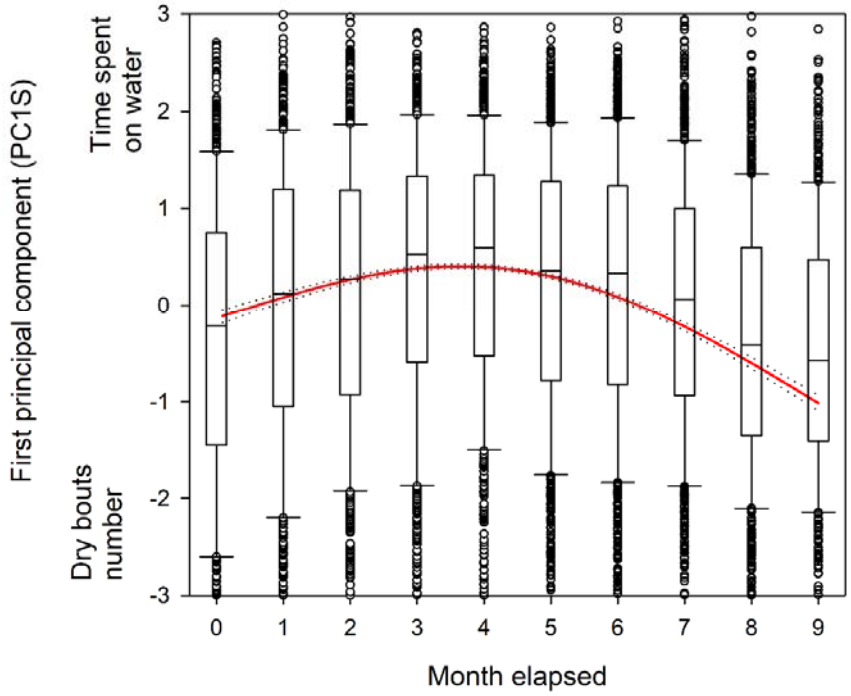


Figure 1b

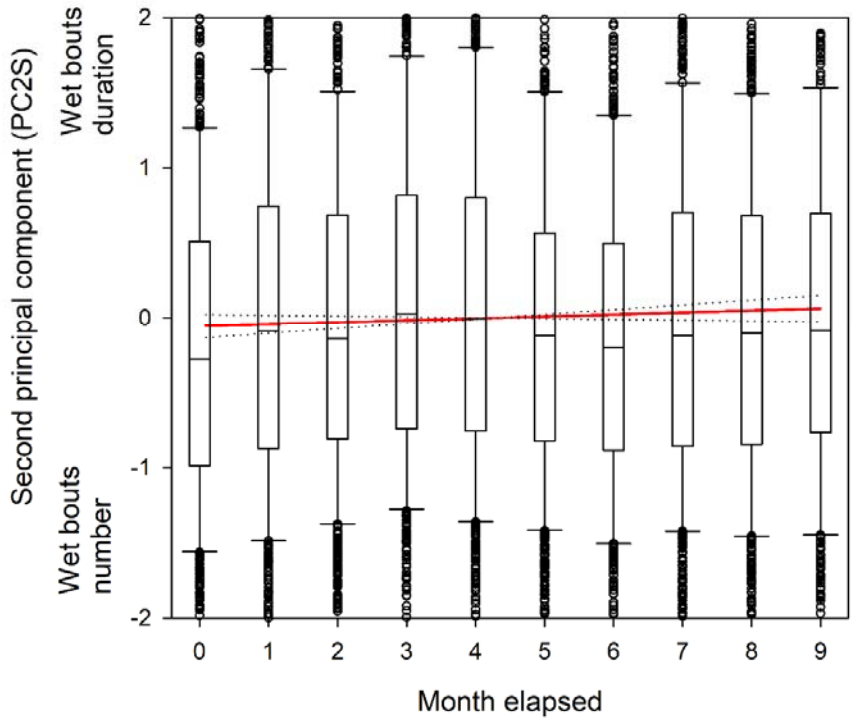


Figure 2a

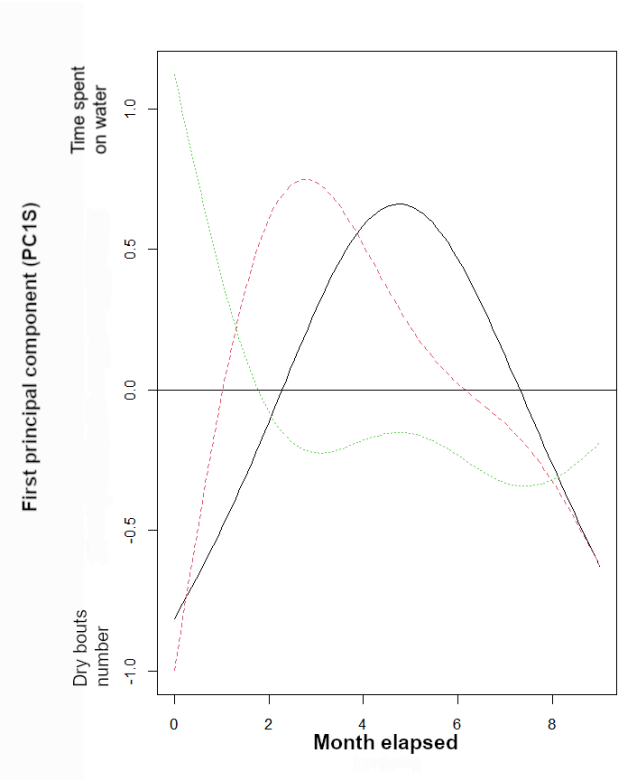


Figure 2b

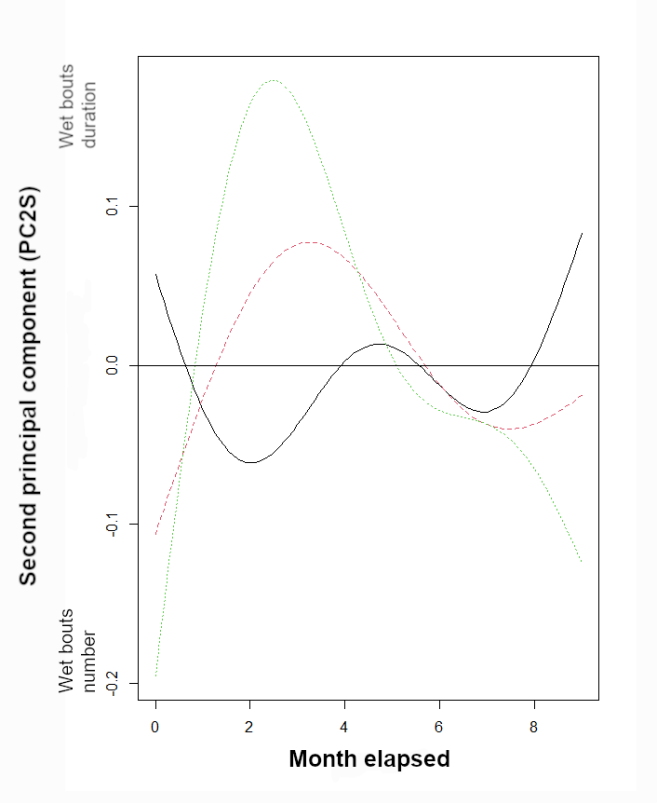


Figure 2c

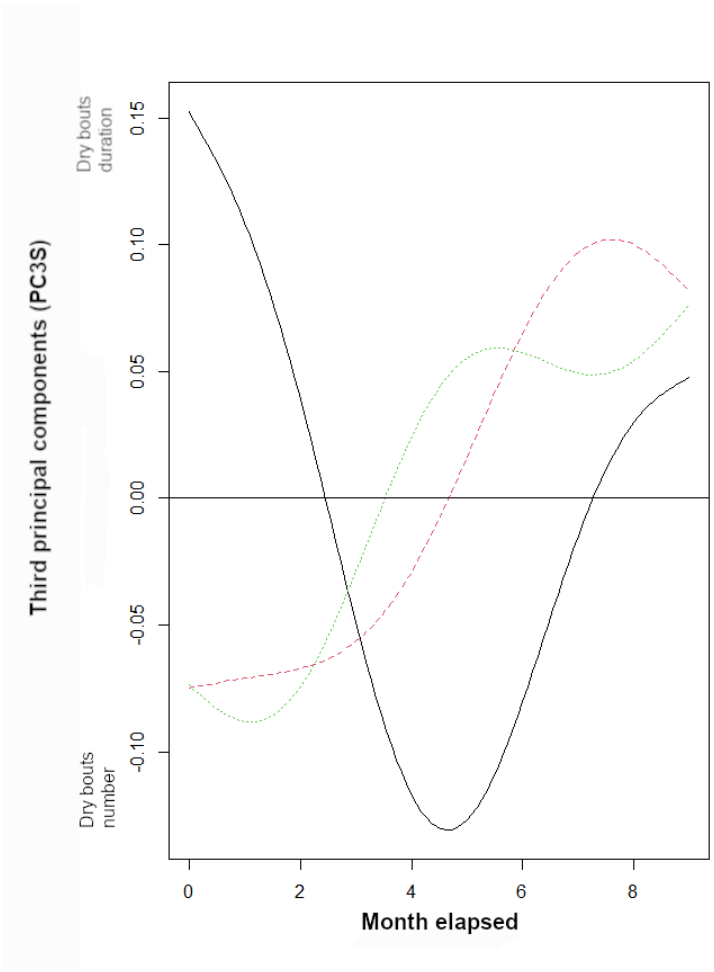

Third principal components (PC3S)
Dry bouts duration
Dry bouts number
0.15
0.10
0.05
0.00
-0.05
-0.10
0
2
4
6
8
Month elapsed

Figure 3a

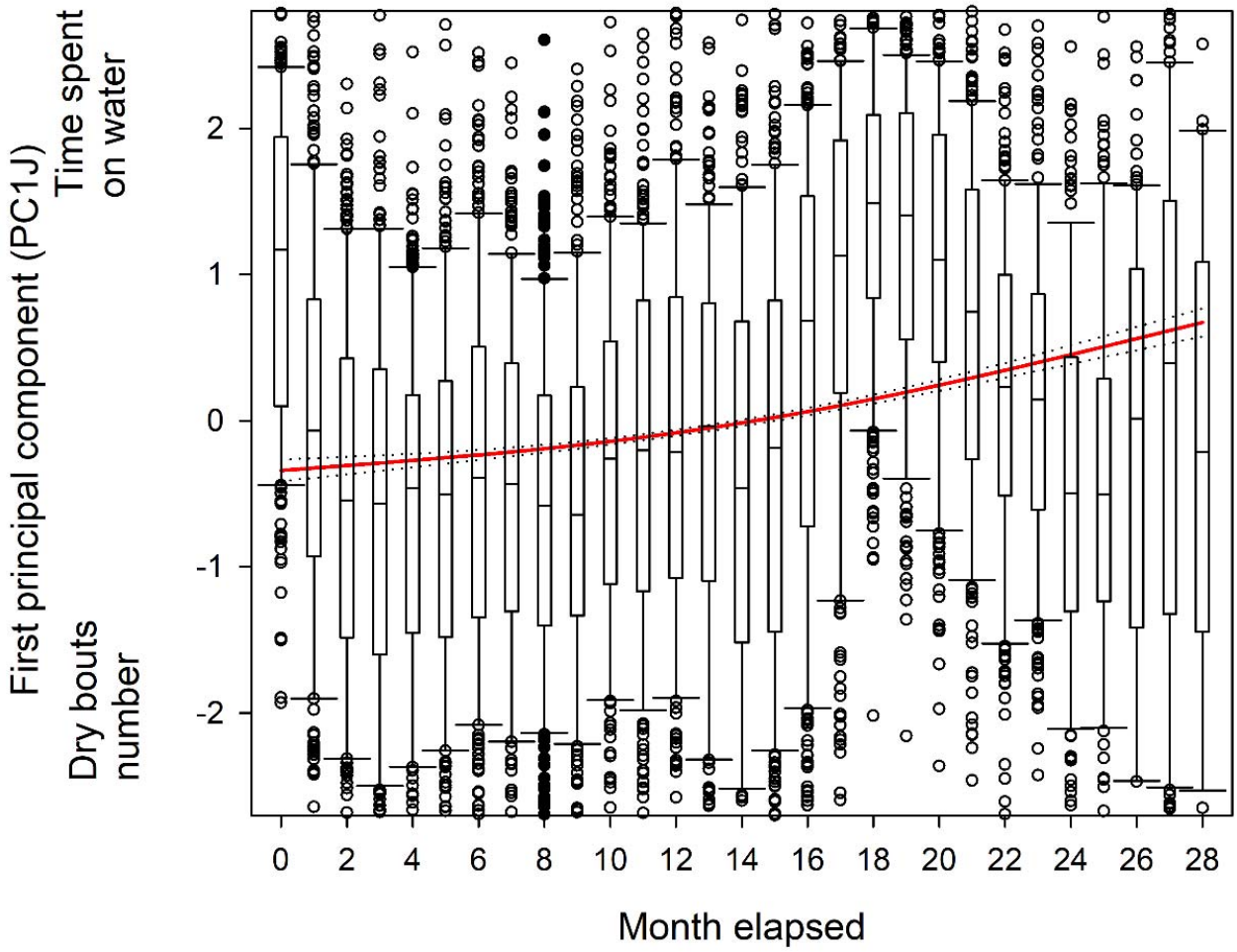
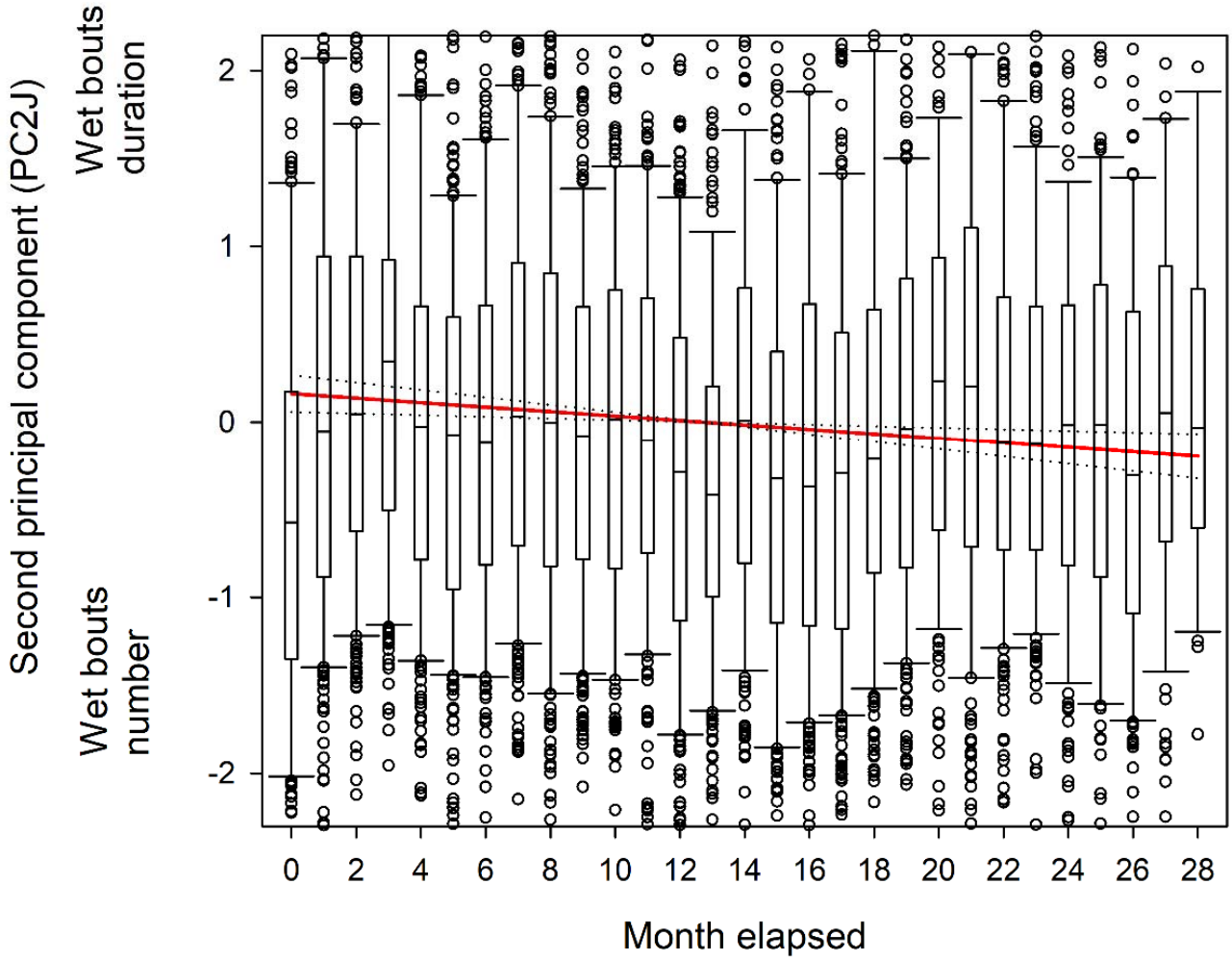

First principal component (PC1J)
Time spent on water
Dry bouts number
2
1
0
-1
-2
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Month elapsed

Figure 3b


Second principal component (PC2J)
Wet bouts duration
Wet bouts number
2
1
0
-1
-2
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Month elapsed

Conflict of interest disclosure

We, the authors of this article declare that we have no financial conflict of interest with the content of this article.

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Supplementary

Species biological aspects

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

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

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

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

805 data for southern albatrosses. Furthermore for large sized species (*Diomedea spp.*) the activity data
806 recorded using GLS never suggested it such a compromise. However, adult birds during the non-
807 breeding season appear to spend much more time on the water during winter, suggesting that partial
808 moult may occur at this time, as observed in many other seabird species that have to moult during the
809 non-breeding season and show reduced activity during specific periods that may correspond to moulting
810 (Weimerskirch et al. 2015b, 2020).
811
812 **Statistical analyses**
813 *Variation in activity parameters between stages with time-lag*
814 The visual comparison shown on Figure S11 was statistically tested using generalized additive mixed
815 models (GAMMs, built with the 'gam' function, itsadug and mgcv package, (Lin and Zhang 1999; Wood
816 2015)) with the values associated with the first axe of the PCA as the dependent variable. We ran model
817 testing for variability in activity parameters for all stages combined (PC1Slag; Table S4). We applied time
818 lag as illustrated in Figure S11, the first axe was modelled as a function of months spent since departure
819 from the colony (monthelap.lag) with a delay of 16 months.
820
821 *Variation in body size*
822 Differences between sexes in body size measurements were tested using Student's t-tests and Wilcoxon
823 rank tests. We tested independently if each measurement (wing length, tarsus length, bill length, bill
824 depth and body mass) varied according to sex and stage (juvenile and adult). The effects were tested
825 using generalised linear models (GLMs) with a Gaussian family and identity link function (Zuur 2009b).
826 Model validation and model selection were performed following (Zuur 2009b). GLMs tested for effect of
827 sex and stage and T-tests tested the differences of body size measurements between males and
828 females. Although sexes and stages differed for some body size measurements, we could not include

body size as an additional explanatory variable in GAMMs testing for factors of variation in activity patterns due to small sample sizes in each sex and stage category.

Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and bill depth whatever the stage (juvenile or adult; Tables S5, S5-S6). In juveniles, males were ~13% heavier than females, while the difference was not significant in adults (Table S5). The most sexually dimorphic phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they were body mass, tarsus length and bill length.

838 Table S1 Selected models testing for the effects of sex, stage, number of months spent since departure (monthelap: duration elapsed since
839 fledging expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on) on activity parameters
840 of Amsterdam albatrosses

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

841 [1] First, second and third principal component issued from principal components analyses considering i) all stages combined (PCS) and ii) only
842 juveniles (PCJ); [2] Individuals

843 Table S2a GAMM results for the first principal components (PC1S; gamm1 see Table S2) of Amsterdam albatross modelled as a function of

844 months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap):stadeAdult	5.178	24.22	0.000
s(monthelap):stadeimm	7.437	45.66	0.000
s(monthelap):stadejuv	5.568	22.32	0.000

845

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.66	0.08	8.34	0.000
February	-0.28	0.08	-3.43	0.000
March	-0.41	0.09	-4.73	0.000
April	-0.60	0.10	-6.01	0.000
May	-0.33	0.10	-3.19	0.001
June	-0.43	0.10	-4.12	0.000
July	-0.19	0.10	-1.88	0.060
August	0.00	0.10	-0.02	0.985
September	0.02	0.09	0.17	0.862
October	-0.10	0.09	-1.10	0.272
November	-0.18	0.09	-2.03	0.043
December	-0.06	0.08	-0.69	0.489
Immatures	-0.63	0.04	-15.70	0.000
Juveniles	-1.21	0.04	-34.00	0.000
Males	0.23	0.03	7.69	0.000

846

847

848 Table S2b GAMM results for the second principal components (PC2S; gamm2 see Table S2) of Amsterdam albatross modelled as a function of

849 months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

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

850

	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

851

852

853 Table S2c GAMM results for the third principal components (PC3S; gamm3 see Table S2) of Amsterdam albatross modelled as a function of

854 months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

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

855

	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

856

857

858 Table S3a GAMM results for the first principal components (PC1J; gamm4 see Table S2) of juveniles Amsterdam albatross modelled as a function

859 of months spent since departure from the colony (monthelap) and month of the year. Reference value is January.

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

860

	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

861

862

863 Table S3b GAMM results for the second principal components (PC2J; gamm5 see Table S2) of juveniles Amsterdam albatross modelled as a

864 function of months spent since departure from the colony (monthelap) and month of the year. Reference value is January.

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

865

	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

866

867

868 Table S3c GAMM results for the third principal components (PC3J; gamm5 see Table S2) of juveniles Amsterdam albatross modelled as a

869 function of months spent since departure from the colony (monthelap), month of the year and sex. Reference value are January and females.

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

870

	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

871

872

873 Table S4 GAMM results for the first principal components (PC1Slag) of Amsterdam albatross modelled as a function of months spent since

874 departure from the colony (monthelap.lag) with a delay of 16 months (see Figure S11), month of the year, stage and sex. Reference values are

875 January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap.lag):stadeAdult	5.001	49.37	0.000
s(monthelap.lag):stadeimm	4.810	19.39	0.000
s(monthelap.lag):stadejuv	7.643	53.53	0.000

876

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.99	0.08	11.95	0.000
February	-0.53	0.09	-5.79	0.000
March	-1.08	0.09	-11.74	0.000
April	-1.48	0.09	-15.75	0.000
May	-1.23	0.09	-13.59	0.001
June	-1.03	0.09	-11.82	0.000
July	-0.42	0.08	-4.92	0.060
August	-0.07	0.08	-0.90	0.985
September	0.02	0.08	0.28	0.862
October	-0.05	0.08	-0.70	0.272
November	-0.15	0.08	-1.96	0.043
December	0.05	0.08	0.67	0.489
Immatures	-0.81	0.06	-14.24	0.000
Juveniles	-0.74	0.05	-14.71	0.000
Males	0.20	0.03	6.96	0.000

877 Table S5 Body measurements of juveniles and adults Amsterdam albatross and percentage of differences between sexes for each measurement.

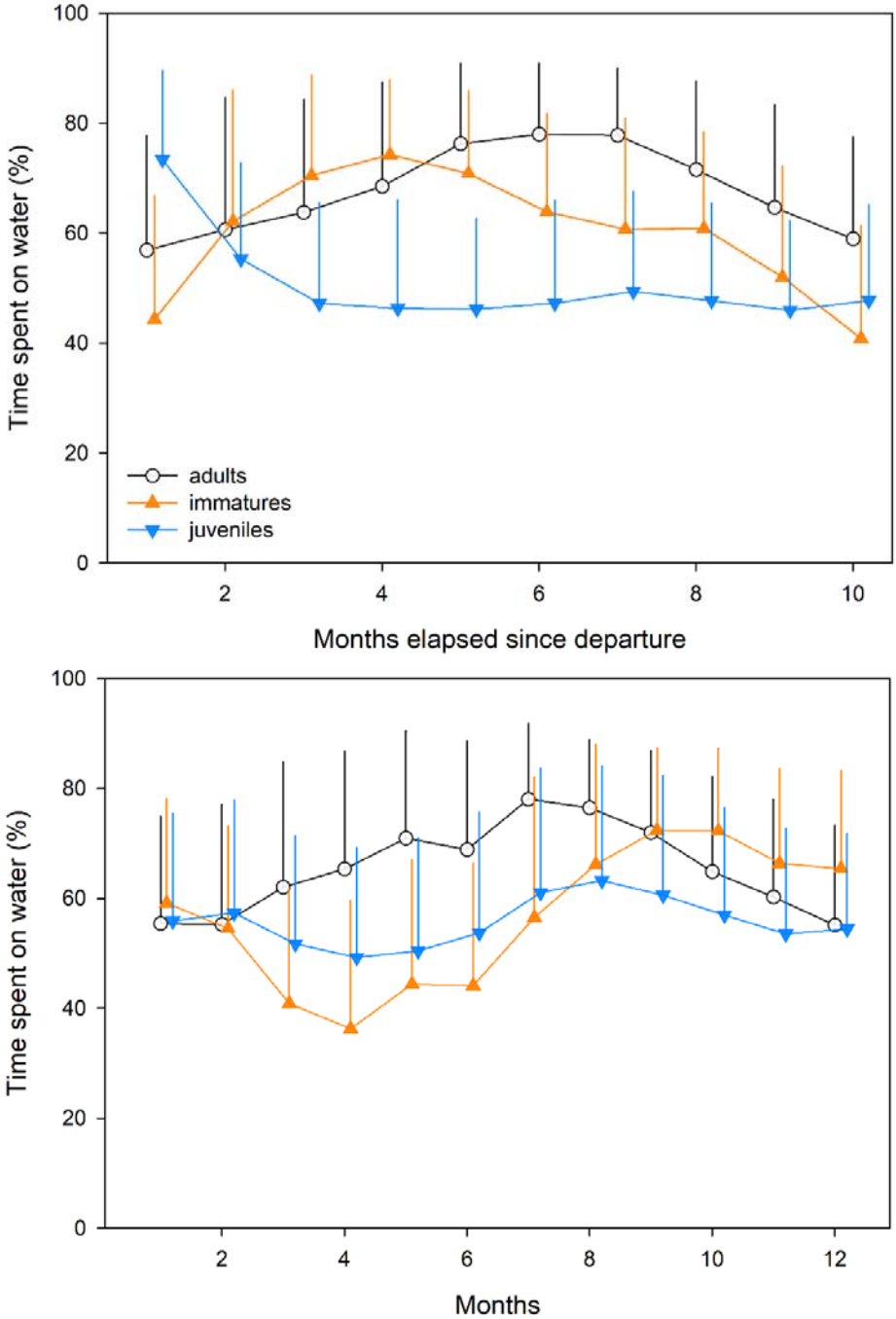
878 Δ is the difference in %, p values are reported

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

879 [1] ratio calculated as Male/Female following Lovich and Gibbons (1992) for species for which males are known to be larger than females cited in (Smith 1999); [2]
880 Student's t-tests used after check for normality of the data for all measurements except for wing length of juveniles (Wilcoxon rank test

881

882 **FIGURES**



883

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

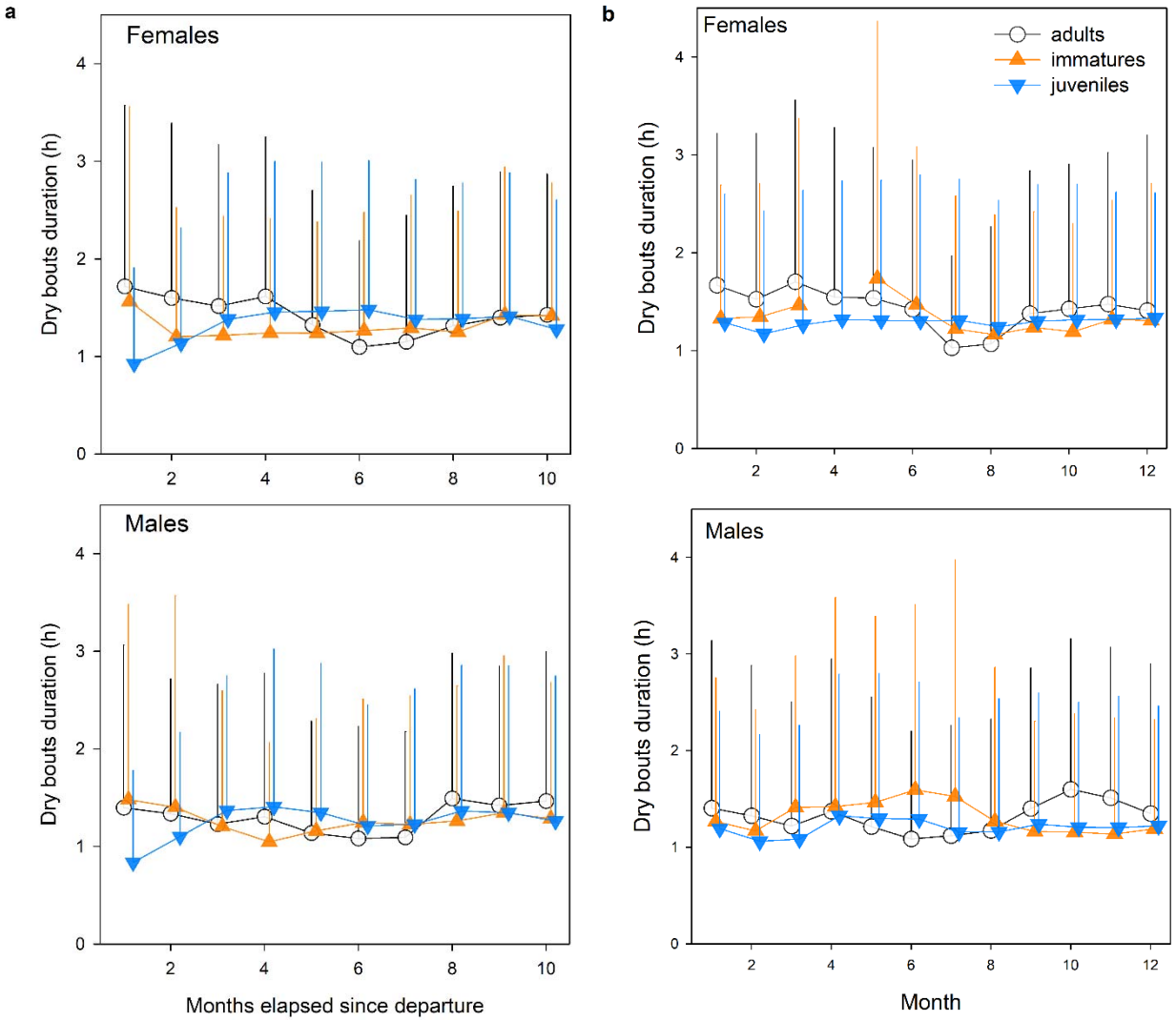


Figure S2 Daily flying bouts duration (dry bouts in hours) depending and on sex (females and males) and on stage (juveniles, immatures and adults) for a) time elapsed since departure from the colony expressed in month (left panel) and for b) each month of the year (right panel). One side error bars represent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

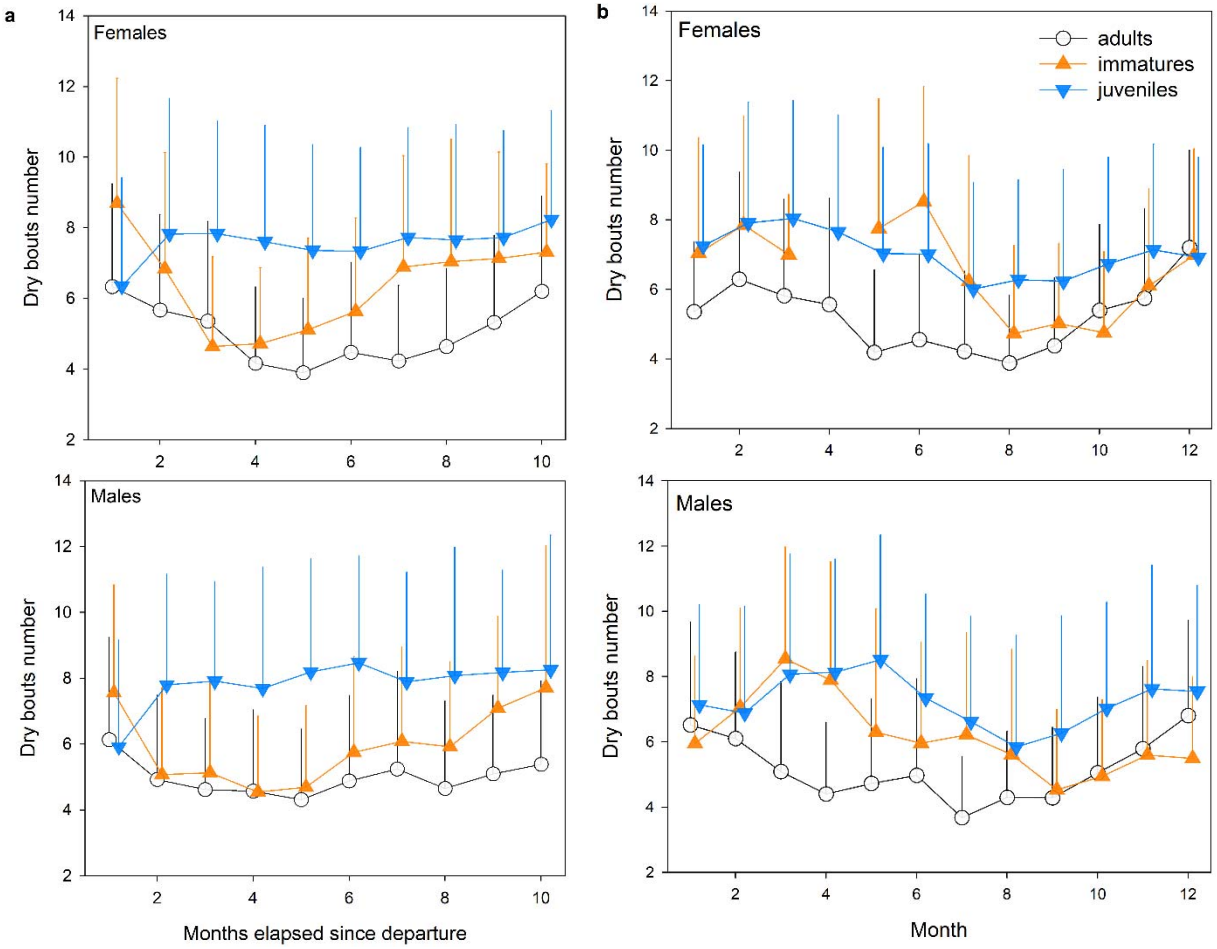


Figure S3 Daily flying bouts number (dry bouts) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

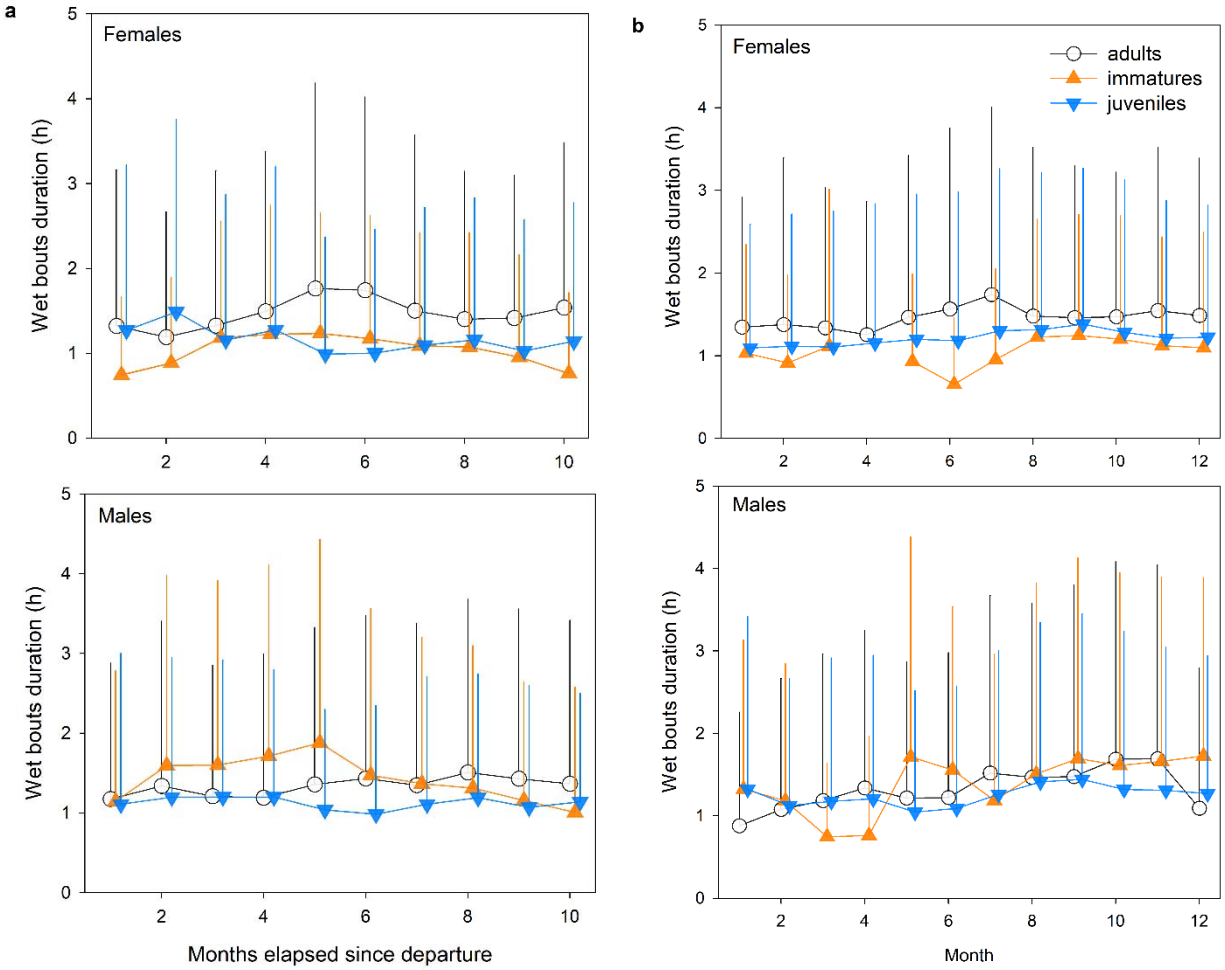


Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures and adults) and on sex (females and males) for every month since departure of the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

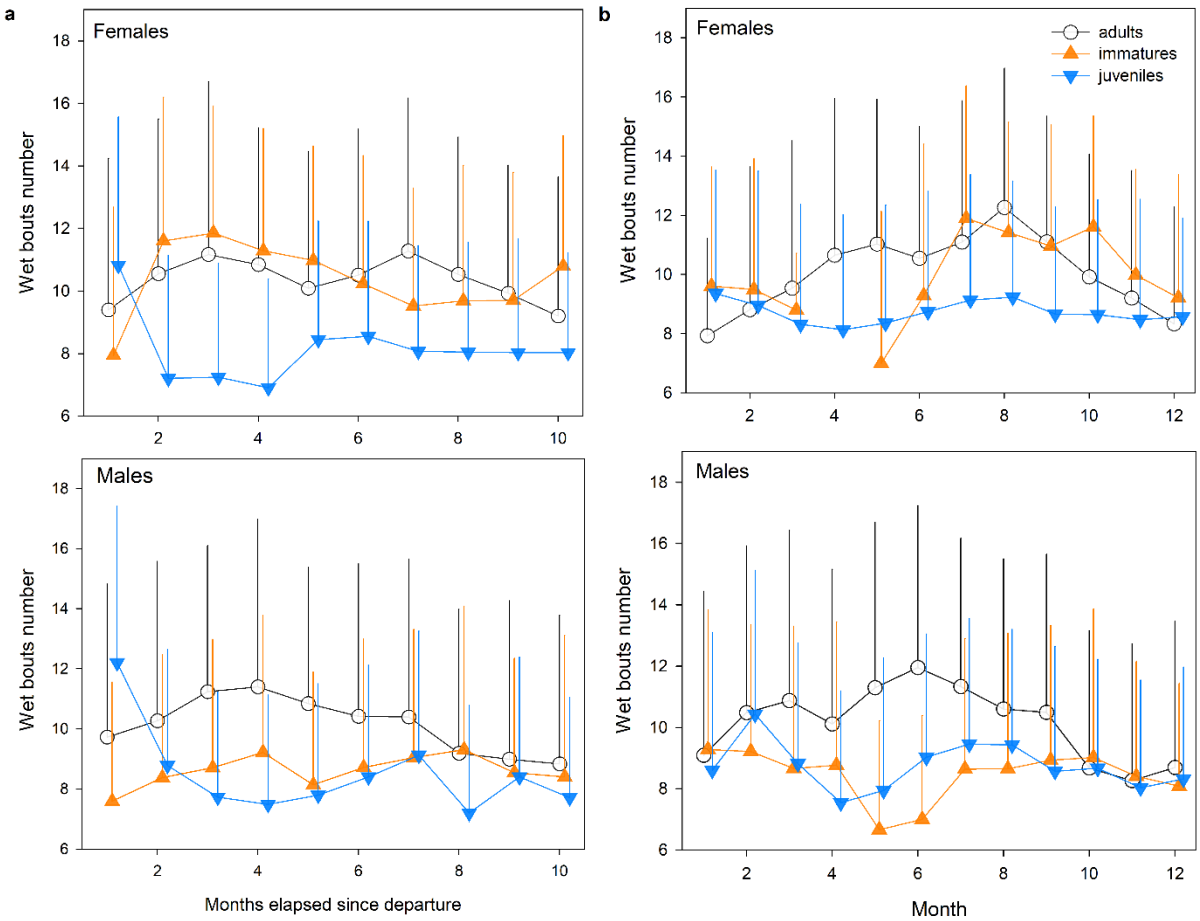
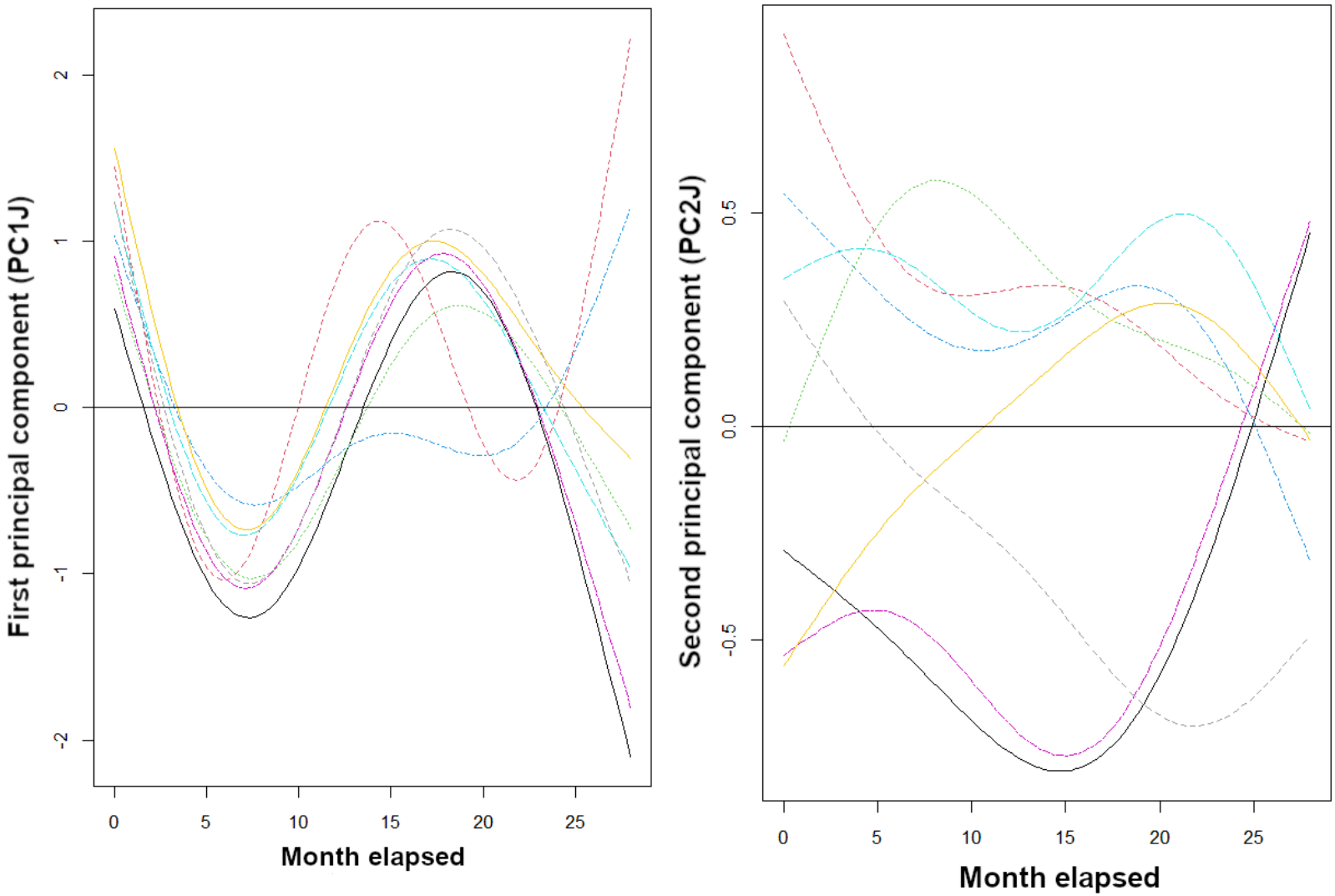


Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd



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906 Figure S6 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of
907 Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs

obtained using random intercepts and slopes (each coloured line representing an individual). Line corresponds to estimated smoother from the GAMM models

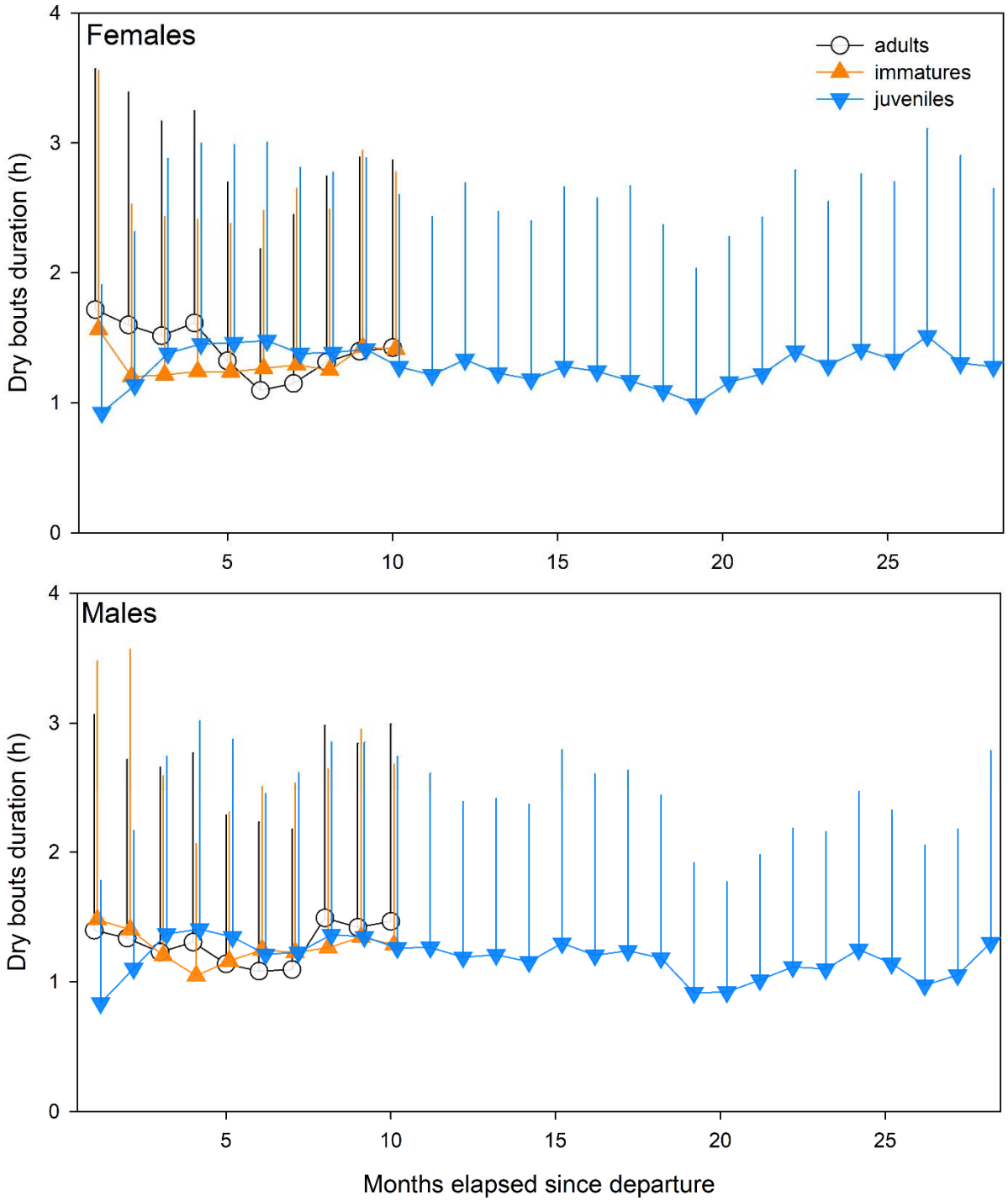


Figure S7 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

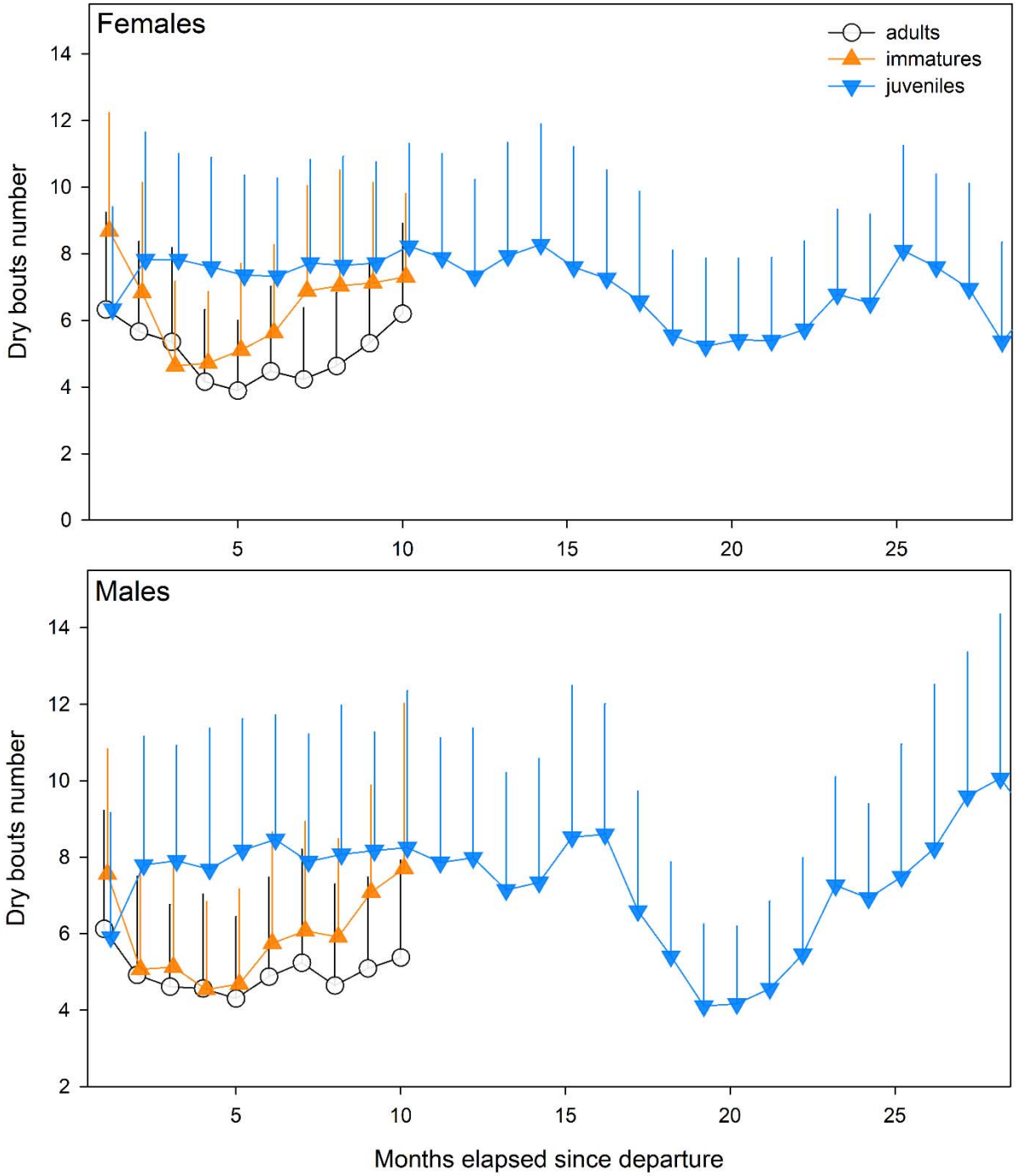


Figure S8 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

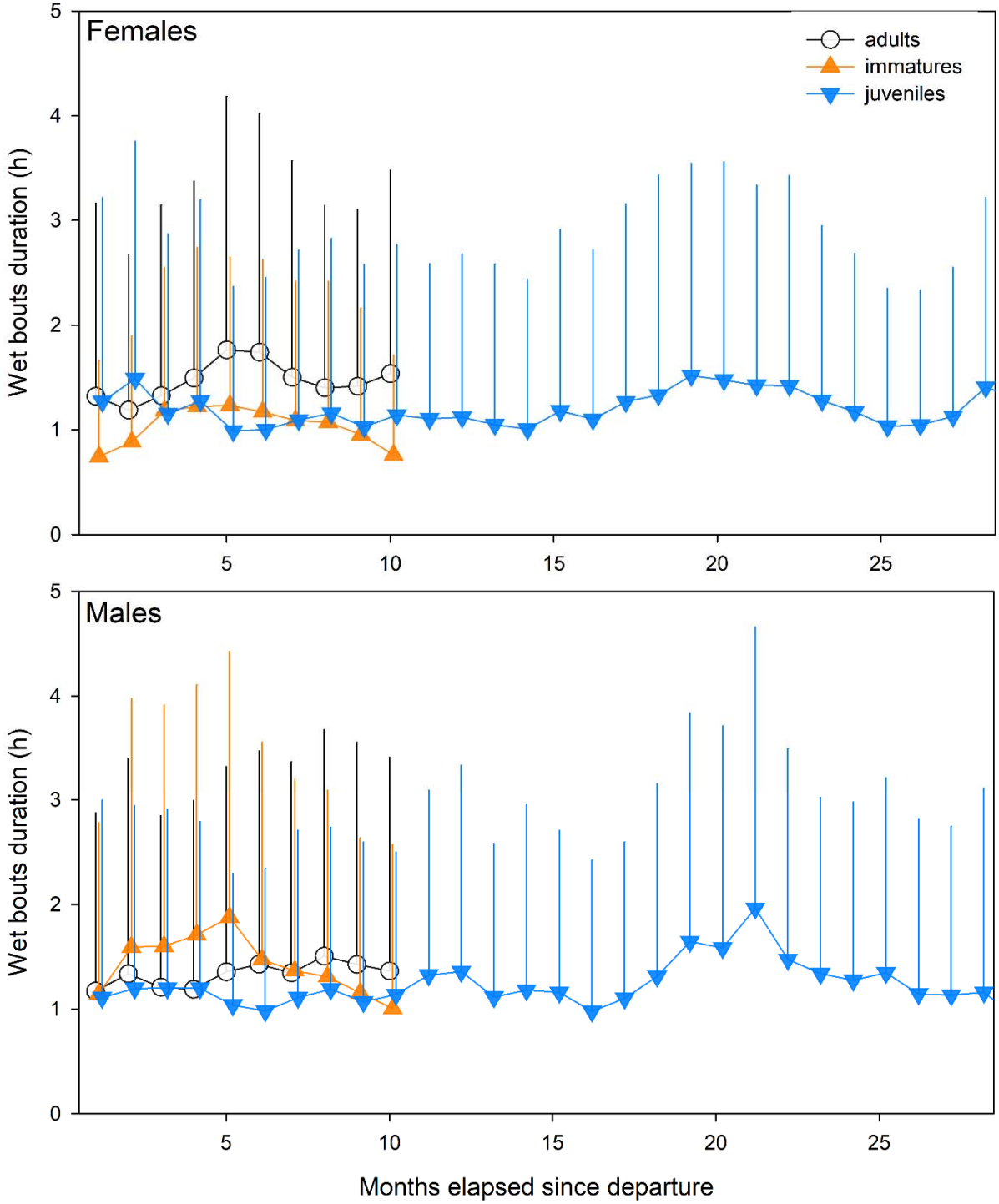


Figure S9 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

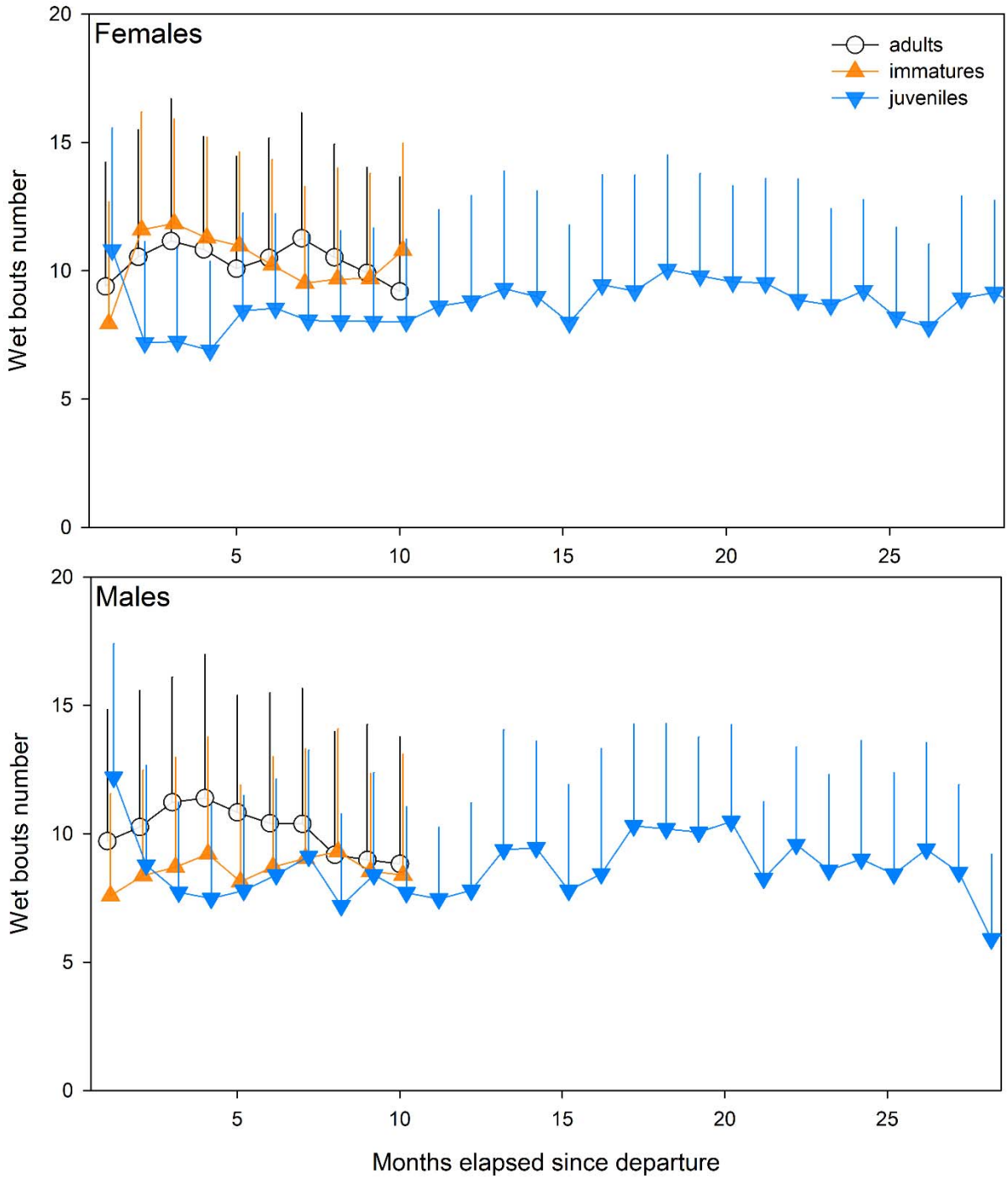
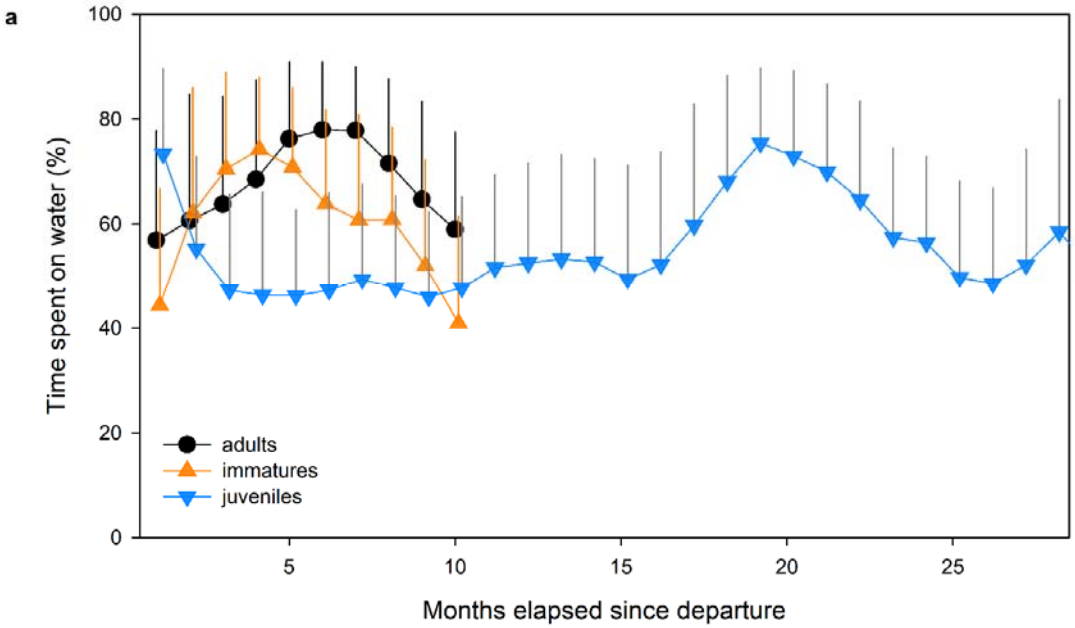


Figure S10 Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd



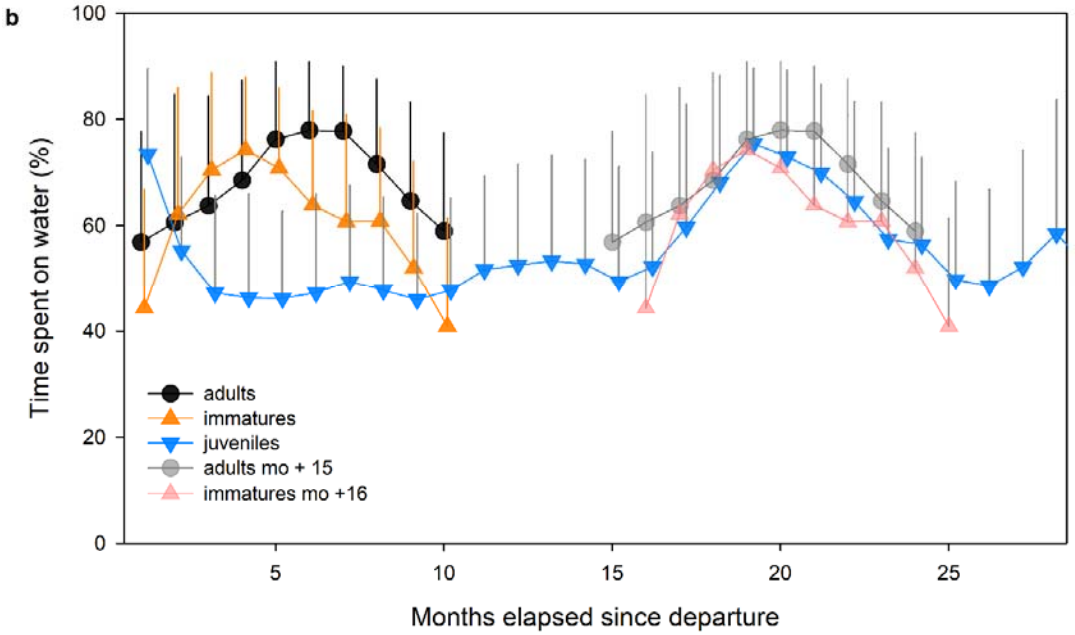


Figure S11 Daily proportions of time spent on water for every month since departure of the colony for juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel) and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error bars represent ± 1 sd

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

Karine Delord, Henri Weimerskirch, Christophe Barbraud

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Submitted by Karine Delord 26 Oct 2021 07:51

Abstract

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

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

Round #3

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by Blandine Doligez, 22 Aug 2023 14:16

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A final minor revision (mostly text edits)

My deepest apologies again for the long delay in sending this decision. I thank the authors for their nice work on this new revised version. I feel that the concerns of the reviewers and myself

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

R: thank you for following the manuscript and for your constructive comments.

Please notice that the line numbers mentioned in the answer refers to the revised version (R3, in track change mode).

- l. 25: replace since by after ?

R: this was changed accordingly. L25

- l. 64: add a coma after “years” and change the parentheses for the reference

R: this was changed accordingly. L64

- table 2: although useful as noted by previous reviews, could be simplified to avoid repetitions for the three different parameters (basically nothing changes but the name of the parameter and direction of expected change). I believe that this table could be drastically reduced

R: the table 2 was accordingly drastically reduced

- table 2 (and/or corresponding text): state clearly that the two hypotheses are not mutually exclusive?

R: this was added in the table and in the corresponding text. L110

- l. 111-116: add (i), (ii) and (iii) before to environmental…, to partial molting… and to sex differences… to clarify the structure of the sentence and ease the reading.

R: this was added. L113-114

- l. 143: what former strategy? I do not understand here; the sentence may need to be clarified here

R: this was clarified. L144

- l. 162: replace “regarding” by “with respect to”? Maybe “year” is also not the right term here since it does not refer to specific years but ages

R: this was modified. L164

- l. 167-168: “data on the three stages over a long period of time”

R: this was modified. L170

- l. 175: so the number of 10 min blocks was divided by 6 to compute a time in hours then?

R: yes exactly

- l. 206: “describe behaviours using gradients of activity” is not so clear to me. Do you simply mean here “changes in behaviour over time and stages”?

R: this was modified. L208

- l. 206 and 208 (and thereafter): not sure the acronyms PCS and PCJ are useful here (you anyway repeat what they correspond each time after, so I would simply remove them). You can then replace PC1S, PC2S etc. by their names directly.

R: we understand that you may find these acronyms unnecessary, but we would prefer to keep them, in particular to facilitate reader’s understanding between the text and the results (text, tables and figures)

- l. 215: double parenthesis

R: note sure to understand the point here because the double parenthesis corresponds to 1) ‘(GAMMs,…’ and to 2) the references ‘(Lin and Zhang 1999; Wood 2015)’

- l. 222: I would add here that interactions between stage and time were included as fixed effects to test for the prediction that differences should vanish with time passed since fledging.

R: this was added in the revised version. L225-227

- l. 231: have you checked whether using AIC corrected for small sample size (AICc) changed anything? If not, I would do it to test for the robustness of the results, as small samples are likely to lead to model overfitting (l. 469 and 477 indicate AICc, but the text mentions AIC?)

R: yes, it has been checked using AICc and the results appeared to be robust compared to those presented in the manuscript. We have therefore chosen to maintain our current presentation. However, if you think it's more correct to present AICc, this can be changed. AICc indications were modified in the revised version.

- l. 235-244: this section appears strange here, as it looks like a simple check of size dimorphism in this species, but with no apparent link to the main question of interest, here

1344 patterns of foraging activity. I would suggest deleting it completely except the sentence
1345 justifying what body size was not included as an explanatory variable (l. 241-244, adding the
1346 actual sample sizes) and move the analyses themselves (description and results l. 294-299,
1347 including table 7) as an appendix.

1348 R: this section was modified accordingly and a reference to the Table 1 was added regarding the sample
1349 sizes. L240-249, 833-849

1350 - l. 253 and 259: you can remove the second "inter-individual variability"

1351 R: removed. L264

1352 - l. 257: replace "found" by "retained"?

1353 R: this was changed in the revised version. L262

1354 - l. 251-252: the interaction was clearly not supported for the second PCA axis for all stages
1355 (table 4 shows a difference of AIC of approx. 1000!) so something is wrong here: only the first
1356 axis is concerned and not the second? Please correct

1357 R: thank you this mistake was changed in the revised version. L256-257

1358 - l. 270 (and 318): I do not think that the word "abrupt" is needed. It may look abrupt
1359 when the whole duration is considered, but may happen gradually during the first month (all
1360 being a question of time scale and reference). You can delete this and simply say "strong
1361 changes". In the same vein, l. 320-321: you mention "also exhibited progressive change" and
1362 "gradual change" but this is quite opposite to abrupt. Please rewrite here for clarity.

1363 R: this was changed and has been rewritten accordingly. L275, L323

1364 - l. 306-308: I would place this sentence at the very beginning of this paragraph (general
1365 presentation of the study)

1366 R: this sentence was moved at the very beginning of this paragraph. L307

1367 - l. 315: "the first months" (plural) – otherwise this is not coherent with the rest of the
1368 sentence

1369 R: this was changed in the revised version. L321

1370 - l. 321: replace "and that" by "so that". Yet, the previous sentences indicate that at least
1371 part of the activity parameters still differ between juveniles and other stages (proportion of
1372 time spent on water), so maybe be a bit more cautious here with respect to similarity?

1373 R: this was changed in the revised version. L328

- l. 326-328: not clear here: are the differences you refer to those observed during the first two months only? As said above, you also mention longer-term differences in this parameter. I think clarification is needed here.

R: this was clarified in the revised. L332-333

- l. 328: a transition here before discussing the interpretation in terms of performance?

R: done L.334

- l. 437: provide permit numbers here

R: done L.437

- l. 480: parentheses to be displaced around references

R: this was changed in the revised version. L894

- l. 336: is this really inconsistency? Is it not quite intuitive that immatures may behave "in between" juveniles and adults, and thus resemble the first in some aspects (or ins some periods) and the second in other aspects?

R: this was changed in the revised version. L350

- l. 347: replace "of optimal behaviours" by "leading to sub-optimal behaviour", and place it at the end of the sentence, since it is true for other mechanisms as well? (but be careful not to overinterpret results in terms of performance as noted by the first reviewer on the first version, and as mentioned here a few lines above).

R: this was modified in the revised version. L344

- l. 344-350: I would place this paragraph before discussing the case of immatures (so before l. 333), as you mainly mention juveniles (see l. 349).

R: this paragraph was moved accordingly. L340-346

- l. 353-354: I do not understand this sentence: they behave differently than what: adults? other species? if adults, when? (since you mention that they readily use similar foraging strategies, so they do not behave differently then?). Please clarify here.

R: this was clarified in the revised version. L367-368

- l. 360-361: not sure that the shag example is a good one here, as it does not illustrate the idea of progressive improvement in flight performance, but compensation strategies for lower flight performance instead.

R: this was removed in the revised version. L375

- l. 363: “fly over long distances away from”

R: this was changed in the revised version. L378

- l. 365-367: I would simplify here by saying “The progressive change… could be either due to physical development or experience gain”.

R: this was changed in the revised version. L380-382

- l. 368: “Elucidating the mechanisms of the transition…” would be more correct I think. Also add “however” to show that this remains a important question to tackle?

R: this was changed accordingly in the revised version. L382-383

- l. 373: juvenile

R: this was modified in the revised version. L388

- l. 378 (and 431): renewal or molt?

R: this was modified in the revised version. L393

- l. 386: replace “this” by “the same” or “a similar”

R: this was modified in the revised version. L401

- l. 388: male and female Amsterdam albatrosses

R: this was modified in the revised version. L403

- l. 391-392: I’d suggest “Males in all stages did more bouts on water and juvenile males shorter wet bouts, compared to females”.

R: this was modified in the revised version. L405-406

- l. 391-394: I would place the description of the differences observed between sexes before discussing its origin (thus before l. 388), and make only one single paragraph about sex differences.

R: the paragraph was modified accordingly. L403-409

- l. 396: double parentheses

R: done L413-414

1429 - l. 402-404: this suggests strong selective pressures for decreasing size dimorphism. Are
1430 pressures that maintain this dimorphism known (e.g. sexual selection)? It could be worth saying
1431 a word about it here, as the paragraph ends a bit abruptly otherwise. Also, would a sentence
1432 like "Sex differences in the acquisition of foraging performance during the first months after
1433 fledging yet remain to be explored", to get back to the main question of the paper, namely
1434 ontogeny of this behaviour. Indeed, you did not test for a sex x phase x month elapsed since
1435 fledging interaction (but sample size does of not course not allow it here), which would be
1436 needed to test whether males and females acquire foraging skills with different speed (this
1437 could be expected if lighter females are more efficient?). Well, something like this to finish off
1438 this section would be good!

1439 R: this was changed accordingly in the revised version. L422

1440 - l. 423-424: no need to repeat the stages here I think

1441 R: this was removed. L442

1442 - l. 427: replace "since" by "after"

1443 R: this was changed. L447

1444 - l. 427-428: is it possible to conclude from the results of the study that the lower survival
1445 observed for the first years in this species is unlikely to be fully explained by such an
1446 improvement in foraging ability, since parameters for juveniles reach the values observed for
1447 adults quite rapidly (even though some differences seem to remain longer)? I guess more
1448 detailed information would be needed to say so, especially data on the actual foraging
1449 performance realized (the amount or quality of preys obtained by juveniles), or at least on
1450 actual behaviour (the parameters used here remain rough when it comes to describe the
1451 behaviour itself). I think some kind of further thoughts on the results would be nice here to
1452 provide perspectives for future work or potential consequences for the understanding of the
1453 dynamics / evolution in this species... (and go beyond a simple summary of results!)

1454 R: done L454-461

1455 - l. 433: the "therefore" does not relate to the previous sentence (on sex differences). It
1456 would be better to rewrite here ("Overall", or "As a conclusion"?)

1457 R: this was changed. L452

1458 - l. 434: indicate that this still would need to be confirmed by directly assessing foraging
1459 performance (see above)?

1460 R: this was changed. L454

- l. 491: quite difficult to read (three “of”)… maybe consider rewriting? (“for all stages”?). Also, Figure 2 has three panels (a, b and c), which should be described in the legend.

R: this was modified. L520-521

- l. 492: double parenthesis to remove

R: corrected L522

- when comparing fig. 2a with 3a, and 2b with 3b, I do not understand why the pattern observed for the first 9 months in juveniles does not appear in the longer period. I acknowledge that the smoothing and other parameters of the models differ in both cases, but the decline (for the first PCA axis) and the increase (for the second axis) are not observed at all anymore (instead reverse tendencies appear!), which is confusing. This needs to be explained clearly.

R: if we compare fig 2a (green line for juveniles) with 3a (boxplot values) for the first 9 months the same pattern appeared, in this case high value for the first month declining thereafter. When comparing fig 2b (green line for juveniles) and 3b (boxplot values) over the same period, low value the first month then increasing.

- l. 512 and 516: I guess this is fig 3 not 2?

R: this was changed in the revised version