TITLE

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

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Abstract

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

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

Introduction

The transition from parental food dependency to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals (Mushinsky et al. 1982; Margrath and Lill 1985; Martin and Bateson 1985; Marchetti and Price 1989; Langen 1996; Burns et al. 2004) and is increasingly documented in a wide range of taxa (reptiles, birds, and some mammals). A widely accepted 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. 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 environmental changes occurring throughout the seasons , to partial moulting which is suspected to occur outside the breeding period and to result in reduced activity for adults and immatures (i.e. more time 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 monitored annually since 1983 and all individuals were individually marked (numbered stainless steel and plastic engraved colour bands; see Rivalan et al. (2010) for details). Unbanded birds of unknown age (79 individuals since the

beginning of the study) and chicks of the year were banded, weighed (body mass ± 50 g using a Pesola® spring balance) and measured (wing length ± 1 mm with a ruler, tarsus length, bill length, and bill depth ± 0.1 mm with calipers).

In Amsterdam Island oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder sub-Antarctic waters (Belkin & Gordon 1996). Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021; see Supplementary for species biological aspects). The wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008) referred as '*foraging-in-flight*', the lowest energy consuming feeding strategy. However, this strategy tends to change depending on breeding stage (Phalan et al. 2007; Louzao et al. 2014), and 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; see Supplementary). The immature birds moved widely in longitude (0° to 135° E), exploiting exclusively warm waters 17°-18° C. Juveniles exhibited very large migratory capacities over the southern Indian Ocean after fledging (15° to 135° E, ~ 4500 km from the colony), through a large range of latitudinal gradient (27° to 47° S). 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 secondly performed large-scale movements similar to those of adults during the sabbatical period.

155 GLS are archival light-recording loggers used to study activity of birds over periods lasting up to ~ 2 years.
156 GLSs record the ambient light level every 10 min, from which local sunrise and sunset hours can be
157 inferred to estimate location every 12 h (Wilson et al. 1992). GLS also recorded saltwater immersion data
158 by testing for saltwater immersion at regular interval, storing the number of samples wet (>0) at the end
159 of each 10 min period. We used saltwater immersion to estimate daily activity budget. Despite the higher
160 mean spatial error of location estimates with these devices (over 100 km; Phillips et al. (2004a)), GLS
161 loggers allowed us to track the birds for prolonged periods with minimal disturbance to them. We
162 considered the following stages regarding the year of GLS deployment (see Table 1): juvenile, as a fledgling
163 equipped with a GLS just before leaving the colony for the first time; immature, as a non-breeding young
164 bird that had never bred equipped with a GLS when visiting the colony; adult, as a breeding adult equipped
165 with a GLS during the incubation or brooding period which successfully fledged a chick and thereafter took
166 a sabbatical year. To date, we have retrieved 40 of the 50 GLS loggers deployed in total over 4 years, from
167 which 33 individual tracks were estimated (Table 1). Our original aim was to collect activity data over the
168 three life-stages on a long period of time (>1 year). These data are available from a total of 10 adults
169 tracked throughout their sabbatical period, 13 immature birds and 10 juvenile birds (up to 3.2 years).
170
171 **Data processing**
172 The raw immersion data were values from 0 (no immersion or dry, in flight or sitting on the ground) to
173 200 (permanently immersed in sea water or wet, indicating the number of 3 s periods during 10 min blocks
174 when the sensor was immersed in saltwater). Loggers recorded the proportion of time in seawater at 10
175 min intervals, which we summarized as hours in the water per day (hereafter time spent on water; 10 min
176 blocks immersion data > 0). This measure is a reliable proxy of foraging effort linked to foraging behaviour
177 of the species which enters the water principally to forage (Weimerskirch and Guionnet 2002).
178 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

The aim was to determine whether distinct foraging behaviours could be detected across the patterns of variation of wet/dry data, and then to appraise how these behaviours varied over time and among individuals. First, to deal with the fact that wet/dry metrics were interrelated (number of wet bouts sitting

203 on water and time spent on water, wet bouts duration and dry bouts duration, wet bouts number and dry
204 bouts number) and to avoid redundancy, we ran principal components analyses (PCA built with the 'PCA'
205 function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe behaviours
206 using gradients of activity we ran PCA for i) all stages (PCS; based on activity data collected during the first
207 ten months post-departure) and for ii) juveniles only, as an additional goal was to determine changes in
208 activity patterns during the first two years of life (PCJ; based on activity data collected during the first
209 twenty-nine months post-departure).
210 Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance.
211 For juveniles, the first three principal components (PCJ) explained 92.2% of the total variance. The detailed
212 results of PCA and the variables retained for each axe are summarised in Table 3.
213
214 Second, we used generalized additive mixed models (GAMMs, built with the 'gam' function, itsadug and
215 mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with each of the three first
216 axes of the PCA as the dependent variables. We ran separate models testing for variability in activity
217 parameters i) for all stages combined (PCS) and ii) for juveniles (PCJ), based on different duration of
218 datasets (28 months since departure for juveniles and 9 months since departure for immatures and adults;
219 see Supplementary; Table S1). Thus, for i) we considered the lowest number of months elapsed since
220 departure available (9 months since departure). Months elapsed since departure (the duration elapsed
221 since fledging expressed in month, i.e. the first month after fledging and so on), month of the year (i.e.
222 January and so on), sex, and stage (only for i)) were included as fixed effects. To test for the importance
223 of individual variability in our results we built models with or without random effects. We compared
224 models without random effect, models with random intercepts, and models with random slopes and
225 intercepts to test whether the rate of change of activity parameters as a function of time elapsed since
226 departure varied between individuals (Zuur 2009a). Models included month elapsed since departure as a

227 continuous covariate modelled with non-parametric smoothing functions (Wood 2017). We limited the
228 amount of smoothing (k) with the 'gam.check' function following Wood (2017) for each spline to avoid
229 excessive flexibility and model overfitting that would have no ecological meaning. Models including all
230 combinations of explanatory variables and random effects were then tested and ranked using their Akaike
231 Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach
232 (Burnham and Anderson 2002). The model with the lowest AIC was considered as the best model. Two
233 models separated by a difference in AIC values of less than 2 were assumed to fit the data similarly.
234
235 *Variation in body size*
236 Differences between sexes in body size measurements were tested using Student's t-tests and Wilcoxon
237 rank tests. We tested independently if each measurement (wing length, tarsus length, bill length, bill
238 depth and body mass) varied according to sex and stage (juvenile and adult). The effects were tested using
239 generalised linear models (GLMs) with a Gaussian family and identity link function (Zuur 2009b). Model
240 validation and model selection were performed following (Zuur 2009b). GLMs tested for effect of sex and
241 stage and T-tests tested the differences of body size measurements between males and females. Although
242 sexes and stages differed for some body size measurements, we could not include body size as an
243 additional explanatory variable in GAMMs testing for factors of variation in activity patterns due to small
244 sample sizes in each sex and stage category.
245 Spatial and statistical analyses were performed using R (R Core Team 2021). Values are means ± SD.
246
247 **Results**
248 The most parsimonious models explaining variations in activity parameters in the Amsterdam albatross
249 included time elapsed since departure from the colony, month of the year, stages and sexes (Tables 4 and
250 5; Supplementary Figures S1 - S5; Tables S1), whatever the synthetic activity variables considered (PC1S,

PC2S and PC3S; Table 4). The interaction between stage and time elapsed was significant for the two synthetic activity variables (PC1S, PC2S). 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 found only for two variables (PC2J and PC3J). Selected models also included random effects on intercepts and slopes, indicating inter-individual variability in activity and inter-individual variability in the rate of change of activity as a function of time elapsed since departure from the colony (Supplementary Figures 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 and abrupt temporal changes in activity linked to the time elapsed since departure from the colony in the first two months after fledging (Supplementary Figure 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).

Body size

Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and bill depth whatever the stage (juvenile or adult; Tables 6, S5-S6). In juveniles, males were ~13% heavier than females, while the difference was not significant in adults (Table 6). The most sexually dimorphic

phenotypic traits were body mass, bill depth and tarsus length in juveniles while in adults they were body mass, tarsus length and bill length.

Discussion

Using miniaturized activity loggers (GLS), we showed clear differences and changes in activity characteristics depending on life-stages. 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. 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. 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 month 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 abruptly, with values dropping off in the first two months and then remaining low and overall lower than in adults and immatures. This might indicate a lower foraging activity in naïve birds. During the same period, the duration and number of water bouts also exhibited progressive change. These patterns suggest an early and gradual change in foraging behaviour and that

juveniles progressively behaved similarly to immatures and adults (reaching similar values in activity covariates). 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). However, although the patterns tend to be similar (% time spent on water), there are still some differences between stages (see Supplementary). This seems to indicate that juvenile individuals may have weaker foraging skills during their first two months at sea. Although behavioural changes can often equate to improved performance (e.g. Campioni et al. 2020) this is not always the case. The emergence of juvenile birds as more '*adult like*' in their foraging/flight behavioural patterns is not necessarily a sign of improvement. For example, it could be partly due to individual differences in area use with different environmental conditions encountered (food abundance, wind regimes).

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

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

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

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

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

Temporal changes and sex differences in activity

The temporal variability of activity was found whatever the life-stage considered. Part of the activity changes observed following the departure of juveniles Amsterdam albatrosses may illustrate the swift change in travel and movement behaviour, reflecting a more '*adult-like*' behaviour, not indicating necessarily an improvement of flight performances and of the ability to cope with changing (i.e. increasing wind speed) wind conditions (Sergio et al. 2014), a key parameter for soaring seabirds such as albatrosses. Both extrinsic (i.e. environmental conditions) and intrinsic (i.e. energetic demands linked to plumage renew) factors could be involved in the modulation of foraging behaviour, which can be reflected in the temporal variability.

Moult is an intrinsically costly process requiring time, energy and nutrients (Langston and Rohwer 1996; Ellis and Gabrielsen 2002), and the annual replacement of flight feathers is crucial to ensure efficiency in both flight and thermoregulation (Murphy 1996; Peery et al. 2008; Gutowsky et al. 2014). Stage-specific and sex-specific differences in moult extent occur in wandering albatross, suggesting important constraints (Weimerskirch 1991; see Supplementary). Adult birds during the non-breeding season appear to spend much more time on the water during winter, suggesting that partial moult may occur at this time (Weimerskirch et al. 2015b, 2020). Interestingly, immature individuals appear to have this peak in time spent on the water in spring, suggesting different timing of moult.

Contrary to the wandering albatross (Weimerskirch et al. 2014), males and females Amsterdam albatross forage in similar oceanic water masses and encounter comparable wind conditions (Jaeger et al. 2013; Thiebot et al. 2014). Therefore, it is unlikely that sex differences in activity parameters were caused by differences in foraging habitats. Males did more bouts on water whatever the stage, and depending on stage, shorter wet bouts (juveniles only) compared to females. Consistently, we found that males flew for

longer periods (dry bouts duration) compared to females. When considering all stages, males spent a higher percentage of time on water compared to females.

Sex-specific behavioural differences are common in sexually dimorphic seabirds, where the smaller sex usually undertakes longer trips (reviewed in Wearmouth and Sims (2008)). Sexual size dimorphism can result in differences in aerial agility, foraging area and behaviour, and provisioning rate and preferred prey (Gonzales-Solis et al. 2000; Phillips et al. 2004b, 2011; Weimerskirch et al. 2009; Austin et al. 2019; Barbraud et al. 2021). It has also been suggested that size matters probably because the smaller and lighter sex has a higher foraging and flight efficiency (Shaffer et al. 2001; Clay et al. 2020), suggesting that lighter and lower wing loaded female wandering albatrosses, compared to males, are probably better able to exploit subtropical and tropical waters where winds are lighter. Following this, it can be hypothesized that female Amsterdam albatrosses have a greater advantage in foraging in the subtropical environment than males.

Individual variability in activity

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

foraging behaviours (Harel et al. 2016; Rotics et al. 2016, 2021; Phillips et al. 2017). Nonetheless, given the small sample sizes these results should be interpreted with caution.

Conclusion

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

Ethics

All work was carried out in accordance with the French Polar Institute (IPEV) ethics committee permits.

Acknowledgements

This study was made possible thanks to all the fieldworkers involved in the monitoring program on Amsterdam albatross, namely Jean-Baptiste Thiebot, Jérémy Demay, Rémi Bigonneau, Romain Bazire, Hélène Le Berre, Marine Quintin, Marine Devaud, Chloé Tanton, Jérémy Dechartre and Anthony Le Nozahic. We acknowledge Dominique Joubert for the management of the demographic CEBC Seabirds database. We are grateful to Richard Phillips, British Antarctic Survey, Cambridge for providing GLS loggers. We thank Bertille Mohring for statistical advices on principal components analyses. We thank our PCI recommender Blandine Doligez and reviewers, Juliet Lamb and an anonymous reviewer for constructive comments on an earlier version of the manuscript.

Funding

This monitoring program was supported financially and logistically by the French Polar Institute IPEV (program 109, PI C. Barbraud/H. Weimerskirch), the Zone Atelier Antarctique (CNRS-INEE), Terres Australes et Antarctiques Françaises.

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.

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

457 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)

458 [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

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

460 number and duration of water bouts) year-round in Amsterdam albatrosses

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

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)	

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

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

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1S)				
M_5	Month elapsed + Month + Stage + Sex + Month elapsed: Stage	Month elapsed: Individual	26461.62	
M_4	Month elapsed + Month + Stage + Sex	Month elapsed: Individual	26852.86	-391.24
M_3	Month elapsed + Month + Stage	Month elapsed: Individual	26889.23	-427.61
M_2	Month elapsed + Month	Month elapsed: Individual	26968.28	-506.66
M_1	Month elapsed	Month elapsed: Individual	27311.97	-850.35
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

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

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

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

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

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

Models	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Proportion of time spent on water (PC1J)				
M_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

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

Table 7 Body measurements of juveniles and adults Amsterdam albatross and percentage of differences between sexes for each measurement. Δ is the difference in %, p values are reported

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

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

FIGURES

Figure 1 Modeled a) first and b) second axis of principal components analysis of activity parameters of 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 first axis of principal components analysis of activity parameters of all stages (i.e. adult (plain black line), immature (dashed red line) and juvenile (dotted green line)) of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model

Figure 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

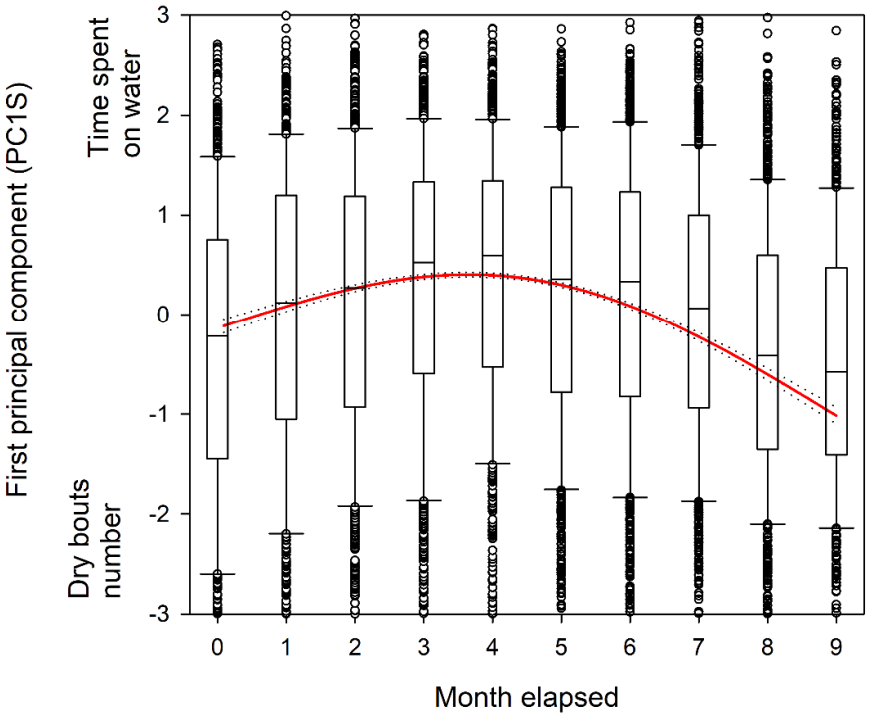


Figure 1b

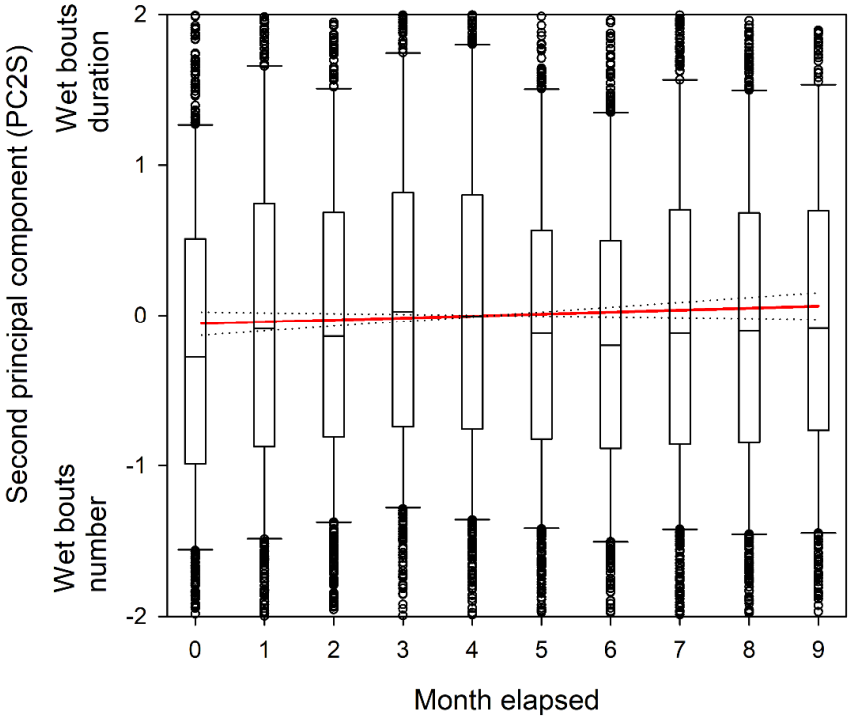
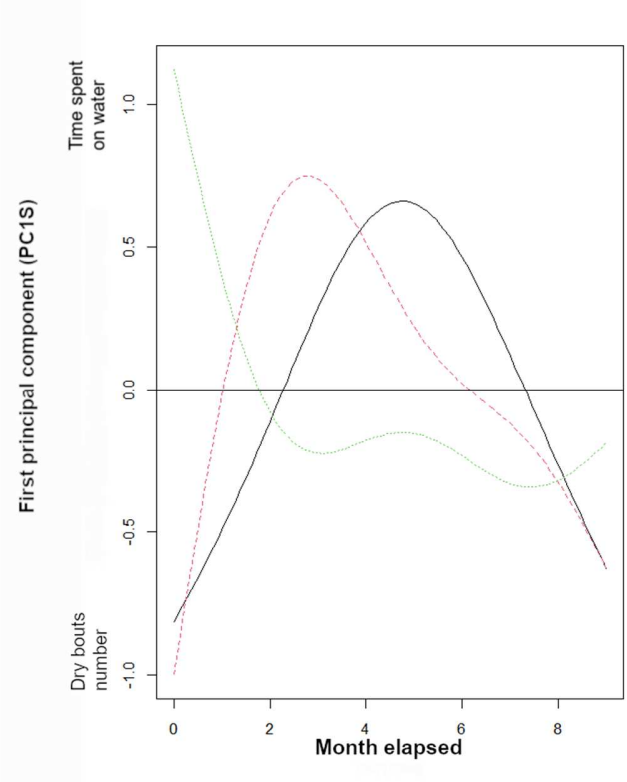


Figure 2a



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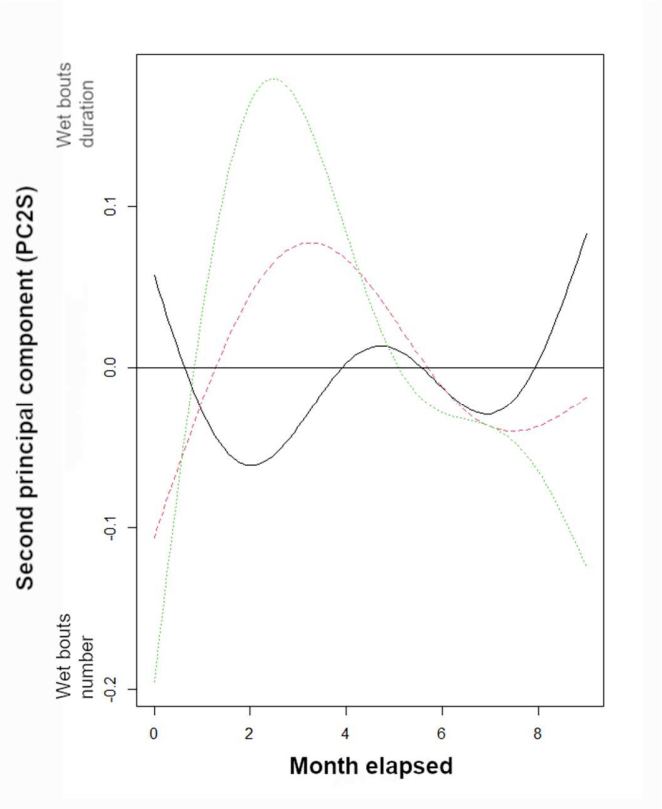


Figure 2c

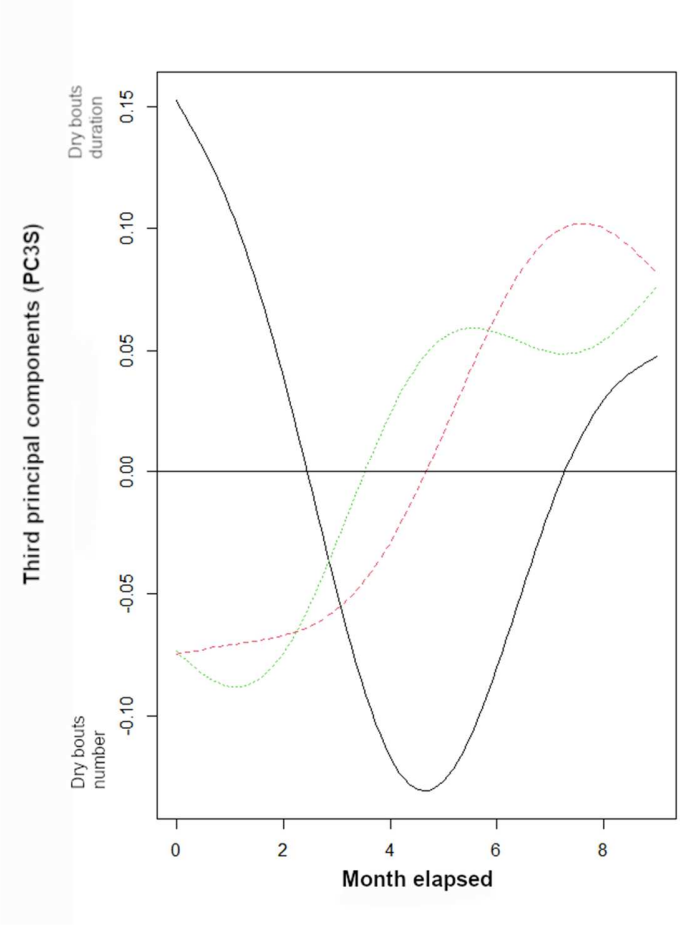

Third principal components (PC3S)
Dry bouts duration
Dry bouts number
0.15
0.10
0.05
0.00
-0.05
-0.10
0
2
4
6
8
Month elapsed

Figure 2a

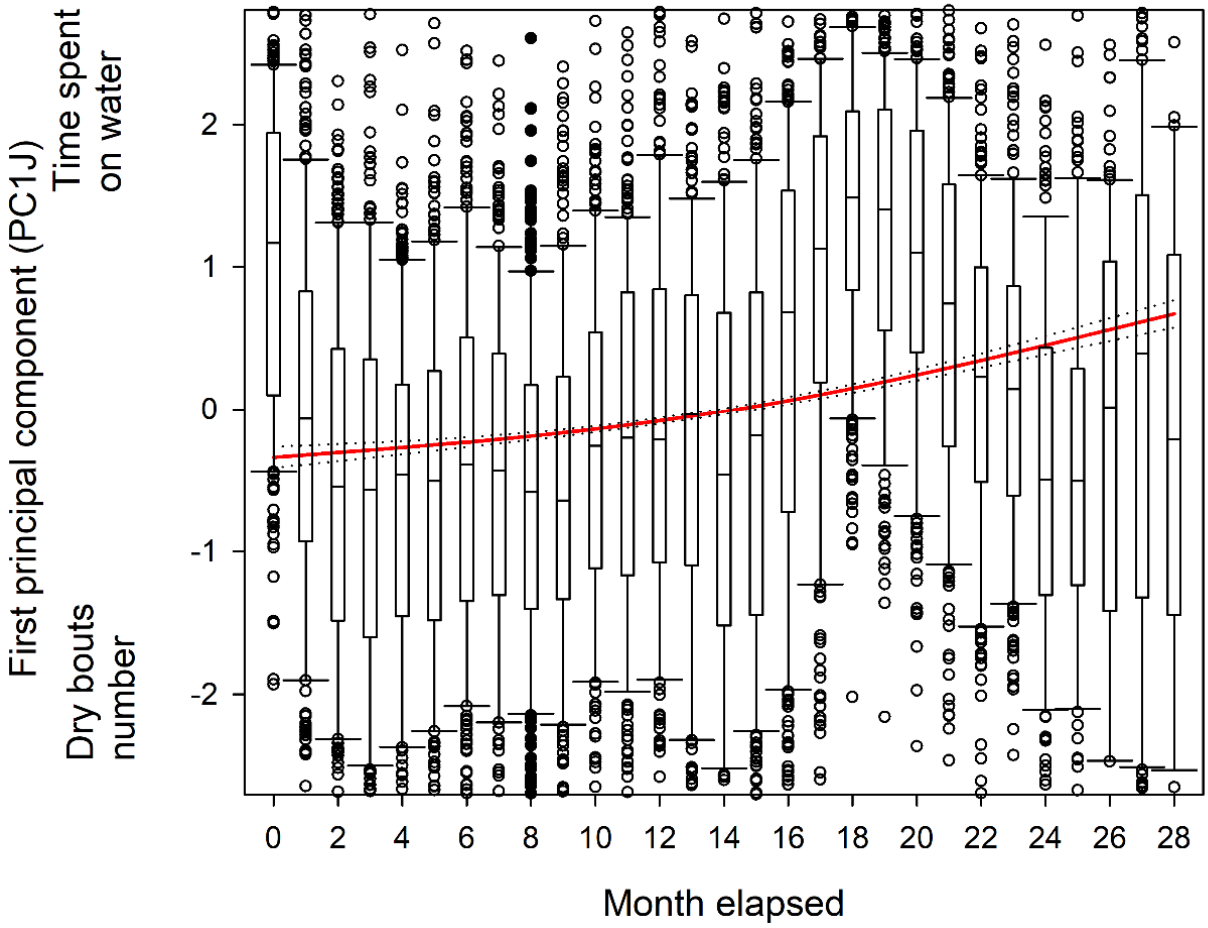
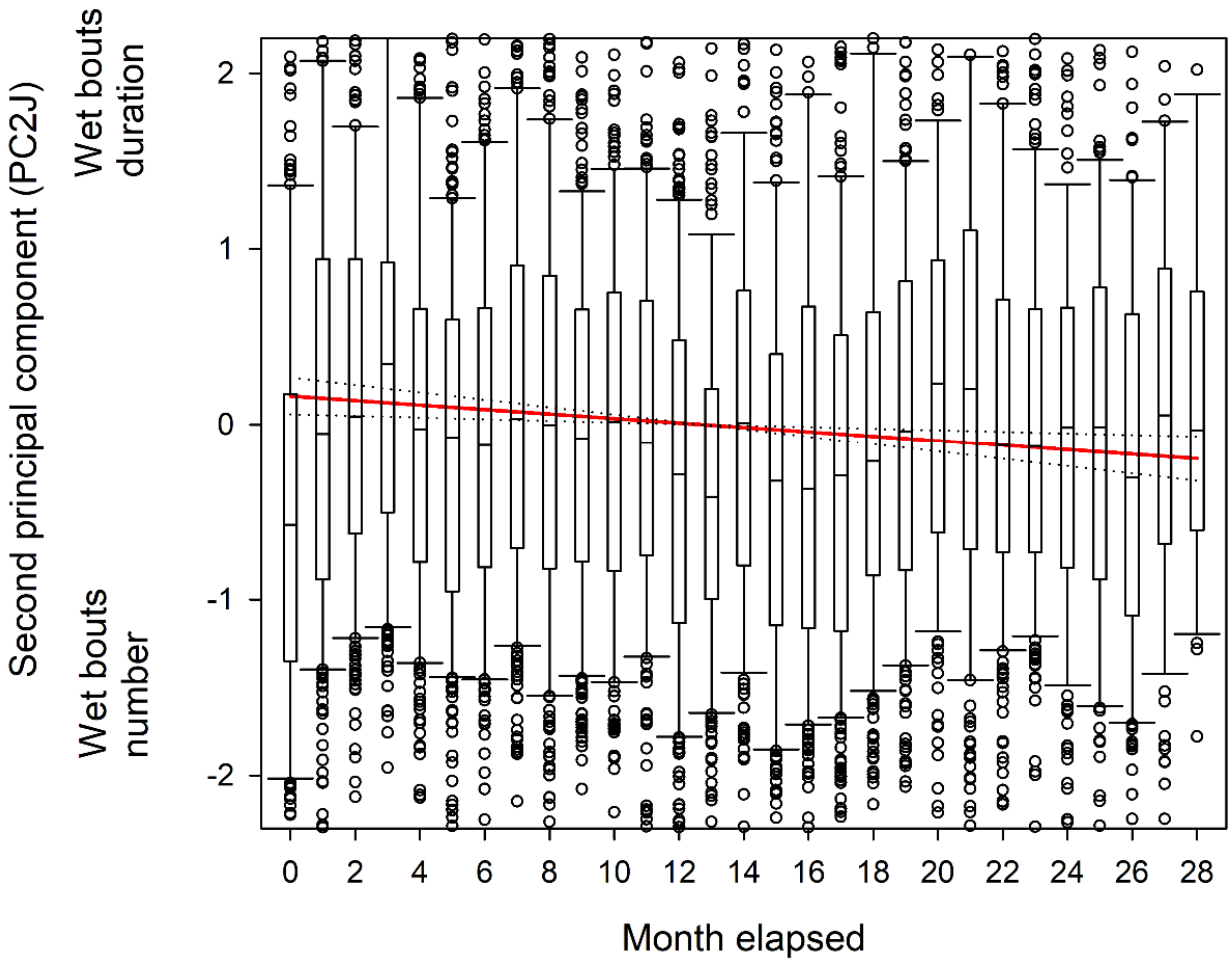

First principal component (PC1J)
Time spent on water
Dry bouts number
2
1
0
-1
-2
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Month elapsed

Figure 2b


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 data for southern albatrosses.

Furthermore for large sized species (*Diomedea spp.*) the activity data recorded using GLS never suggested it such a compromise. However, adult birds during the non-breeding season appear to spend much more time on the water during winter, suggesting that partial moult may occur at this time, as observed in many other seabird species that have to moult during the non-breeding season and show reduced activity during specific periods that may correspond to moulting (Weimerskirch et al. 2015b, 2020).

Statistical analyses

Variation in activity parameters between stages with time-lag

The visual comparison shown on Figure S11 was statistically tested using generalized additive mixed models (GAMMs, built with the 'gam' function, itsadug and mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with the first axe of the PCA as the dependent variable. We ran model testing for variability in activity parameters for all stages combined (PC1Slag; Table S4). We applied time lag as illustrated in Figure S11, the first axe was modelled as a function of months spent since departure from the colony (monthelap.lag) with a delay of 16 months.

817 Table S1 Selected models testing for the effects of sex, stage, number of months spent since departure (monthelap: duration elapsed since fledging

818 expressed in month, i.e. the first month after fledging and so on) and month of the year (i.e. January and so on) on activity parameters of

819 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

820 [1] First, second and third principal component issued from principal components analyses considering i) all stages combined (PCS) and ii) only

821 juveniles (PCJ); [2] Individuals

Table S2a GAMM results for the first principal components (PC1S; gamm1 see Table S2) of Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

Variable	Smoother edf	F-test	p-value
s(monthelap):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

	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

828 Table S2b GAMM results for the second principal components (PC2S; gamm2 see Table S2) of

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

830 (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

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	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

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Table S2c GAMM results for the third principal components (PC3S; gamm3 see Table S2) of Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

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

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

Table S3a GAMM results for the first principal components (PC1J; gamm4 see Table S2) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap) and month of the year. Reference value is January.

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

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

Table S3b GAMM results for the second principal components (PC2J; gamm5 see Table S2) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap) and month of the year. Reference value is January.

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

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

Table S3c GAMM results for the third principal components (PC3J; gamm5 see Table S2) of juveniles Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year and sex. Reference value are January and females.

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

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

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

	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

FIGURES

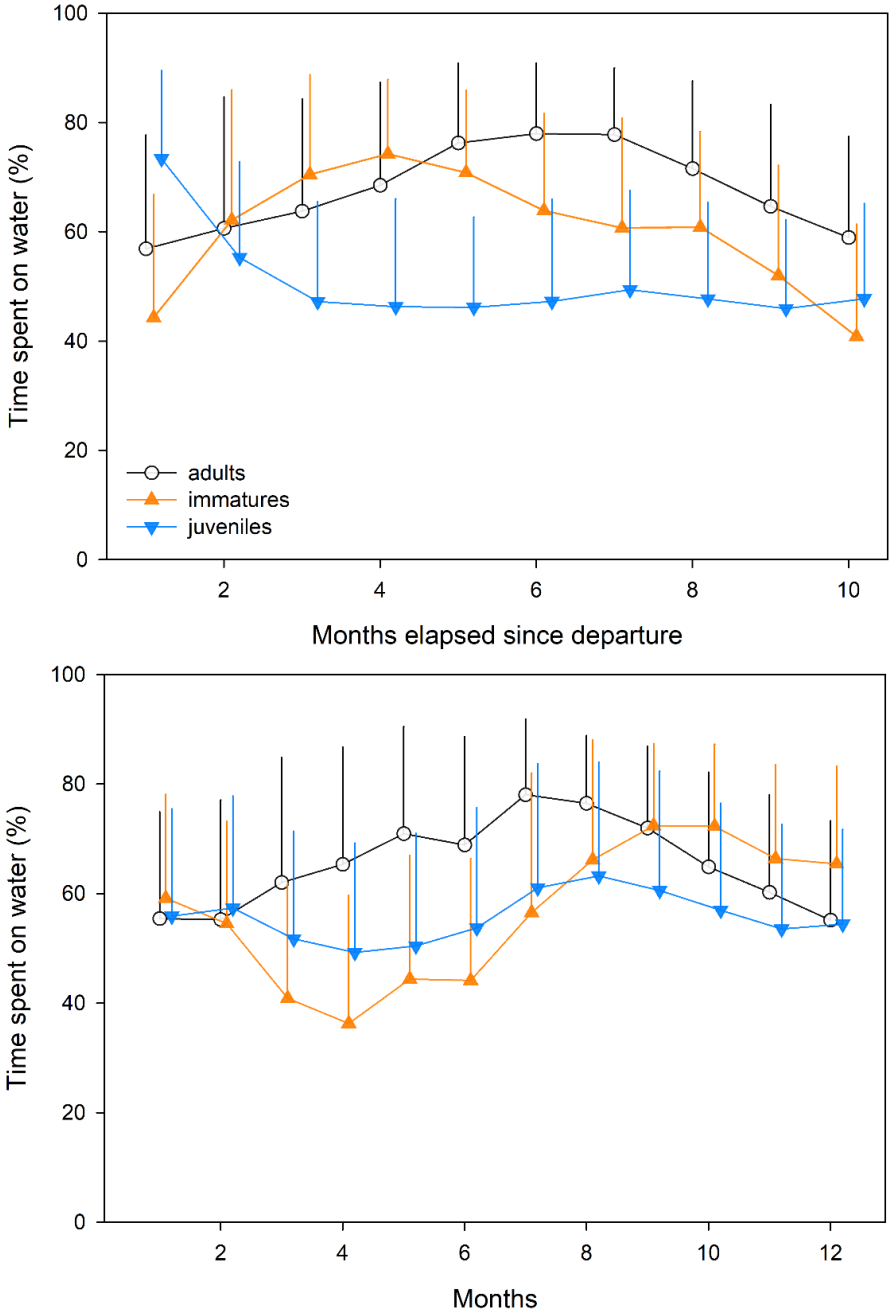

Figure S1 Daily proportions of time spent on water depending on stage (juveniles, immatures and adults) for every month since departure from the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

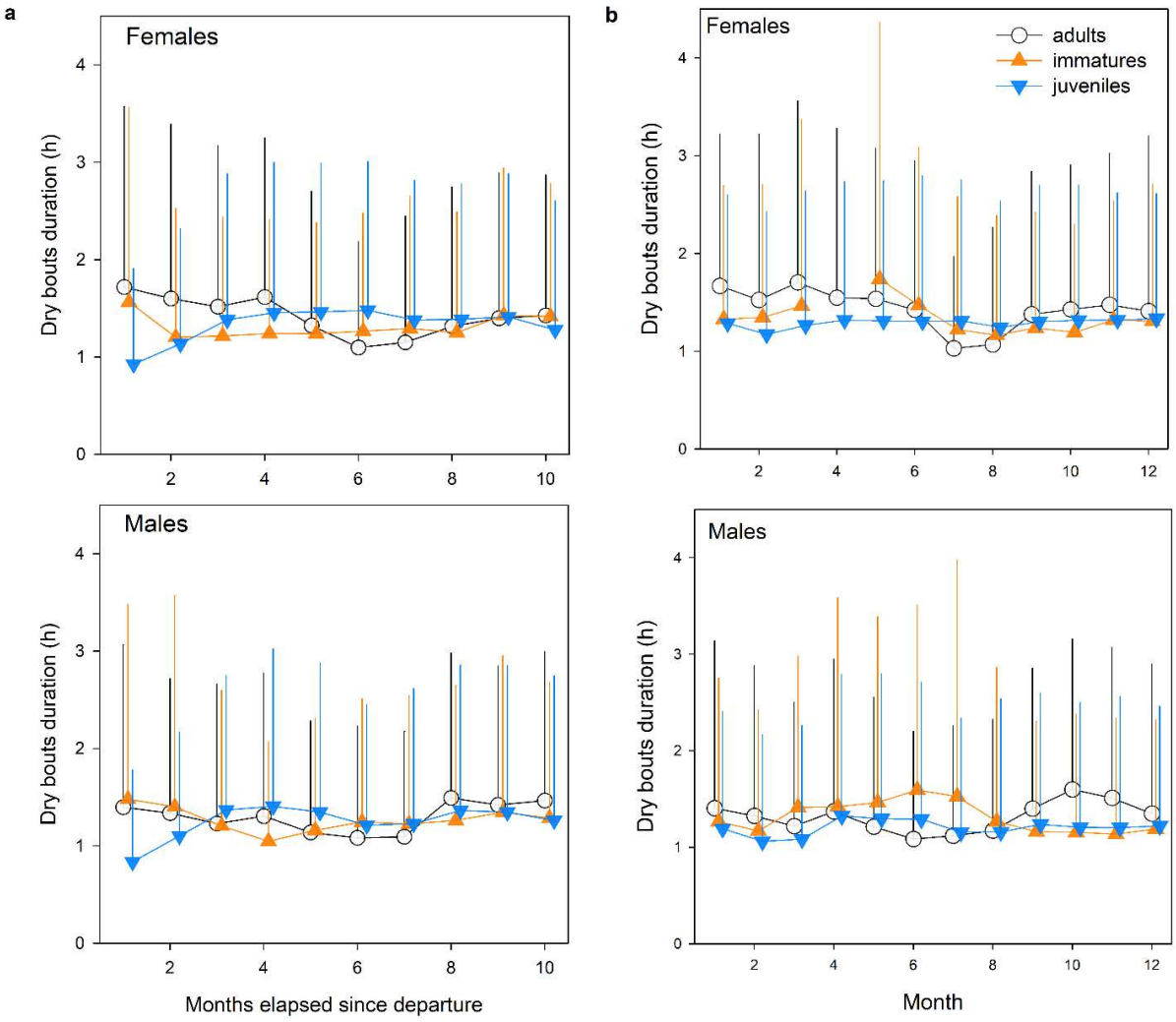

Figure S2 Daily flying bouts duration (dry bouts in hours) depending and on sex (females and males) and on stage (juveniles, immatures and adults) for a) time elapsed since departure from the colony expressed in month (left panel) and for b) each month of the year (right panel). One side error bars represent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

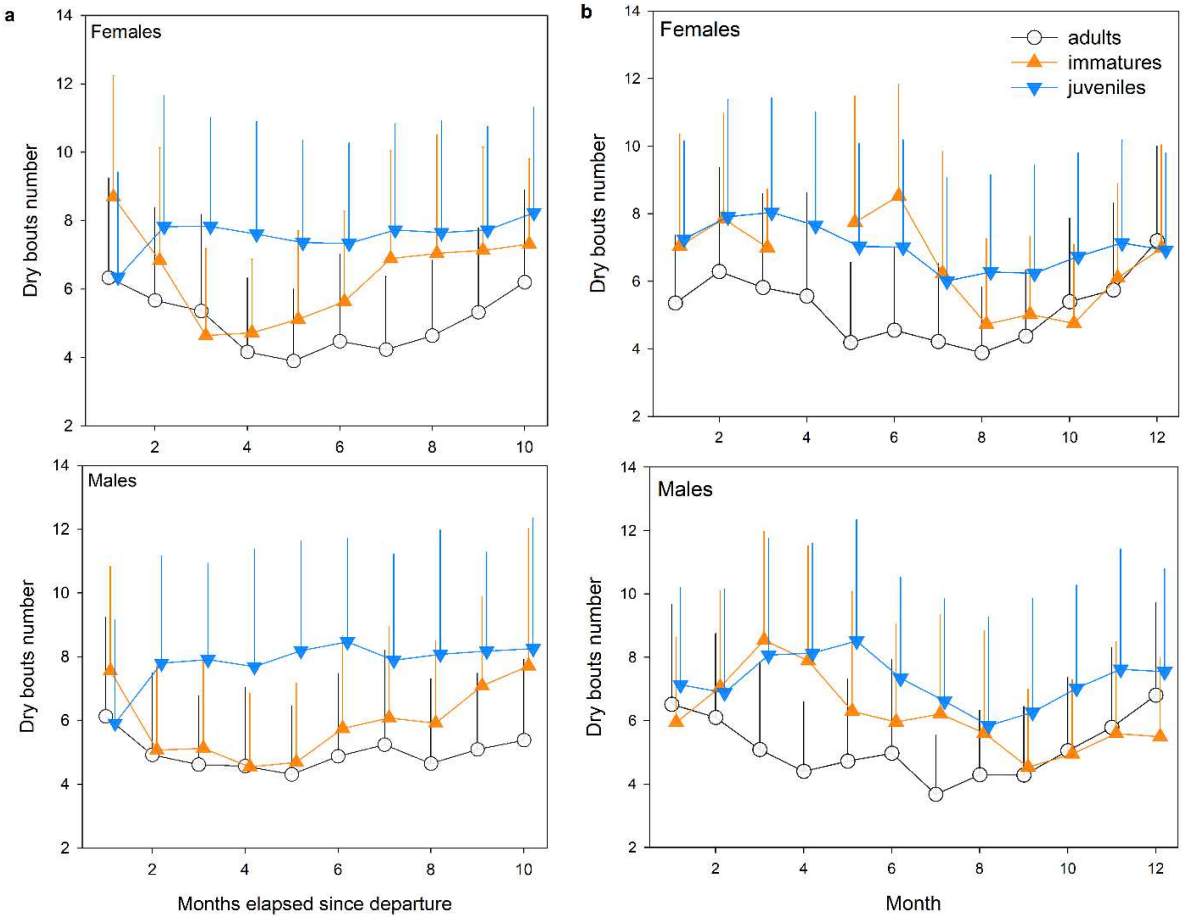

Figure S3 Daily flying bouts number (dry bouts) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

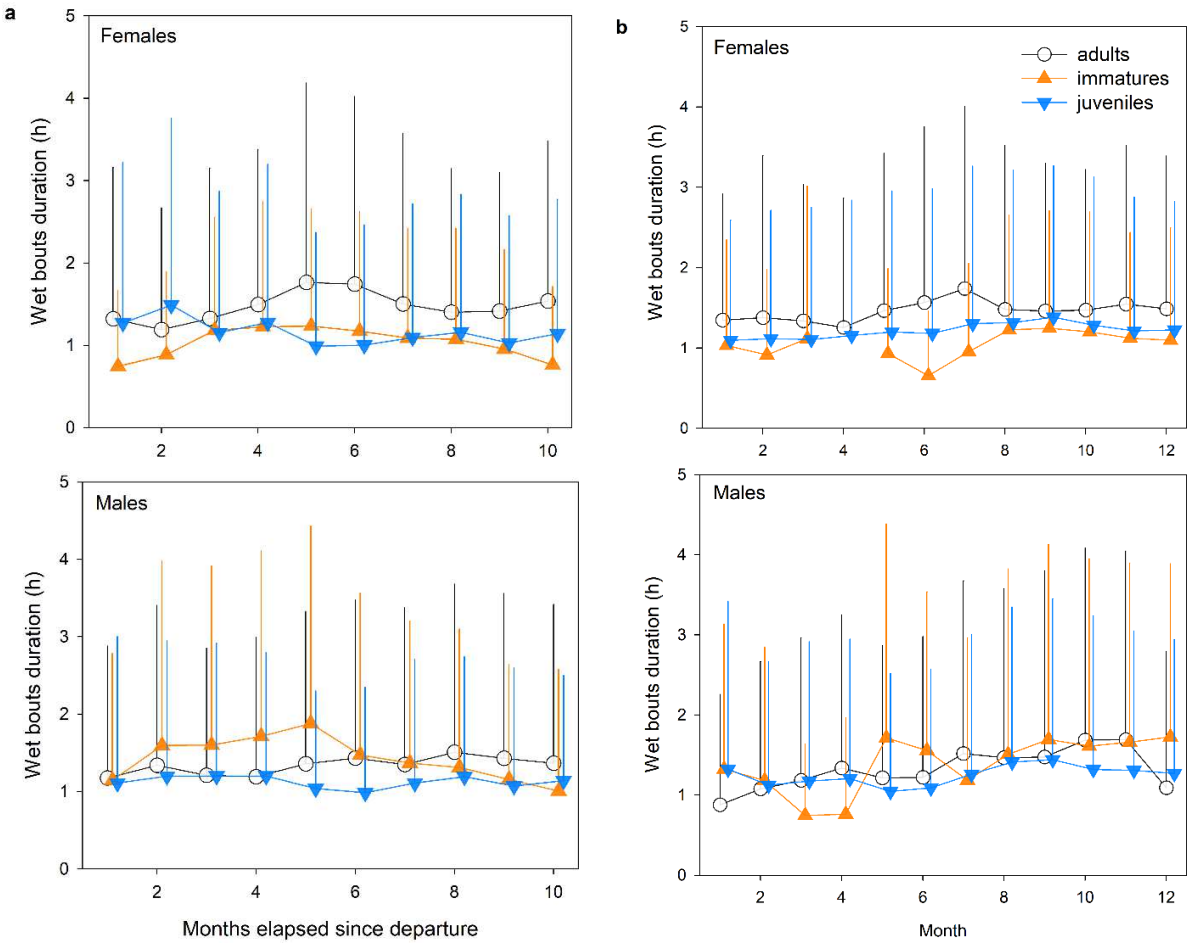

Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures and adults) and on sex (females and males) for every month since departure of the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

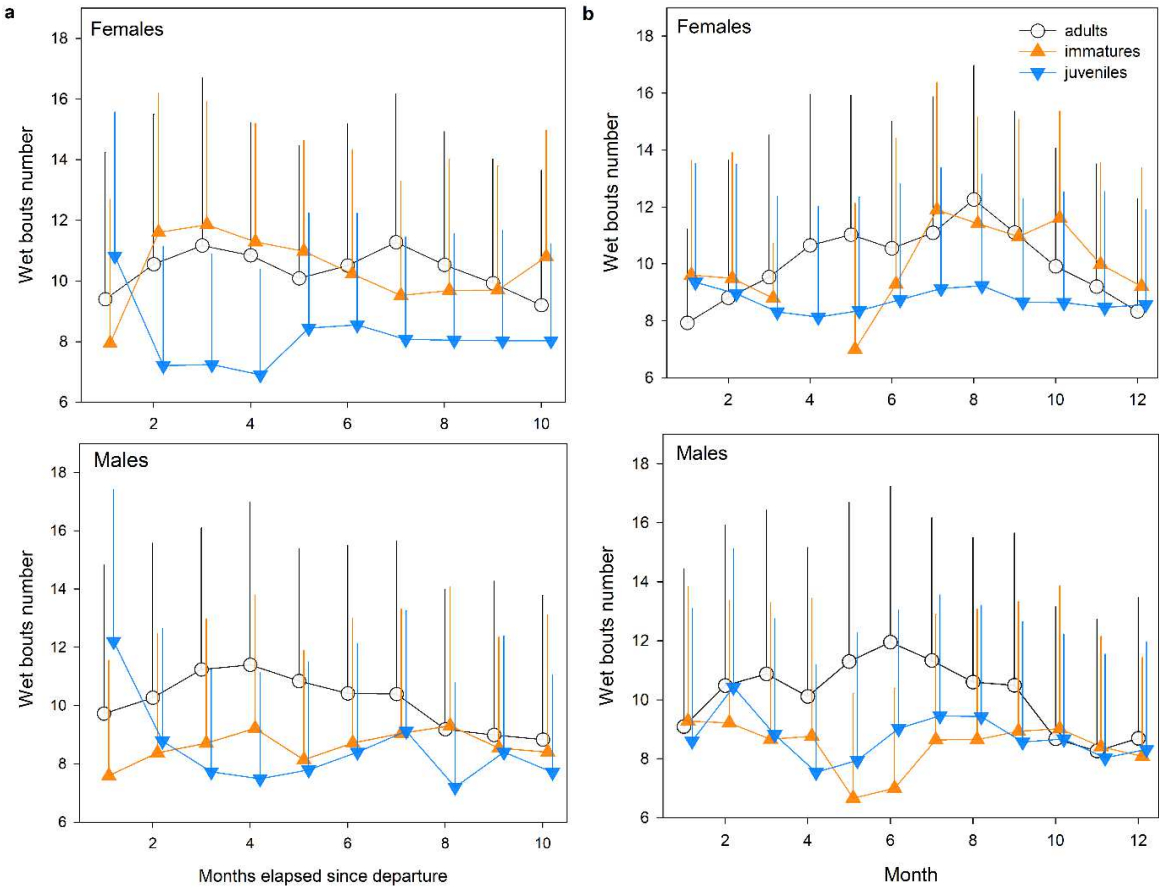

Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

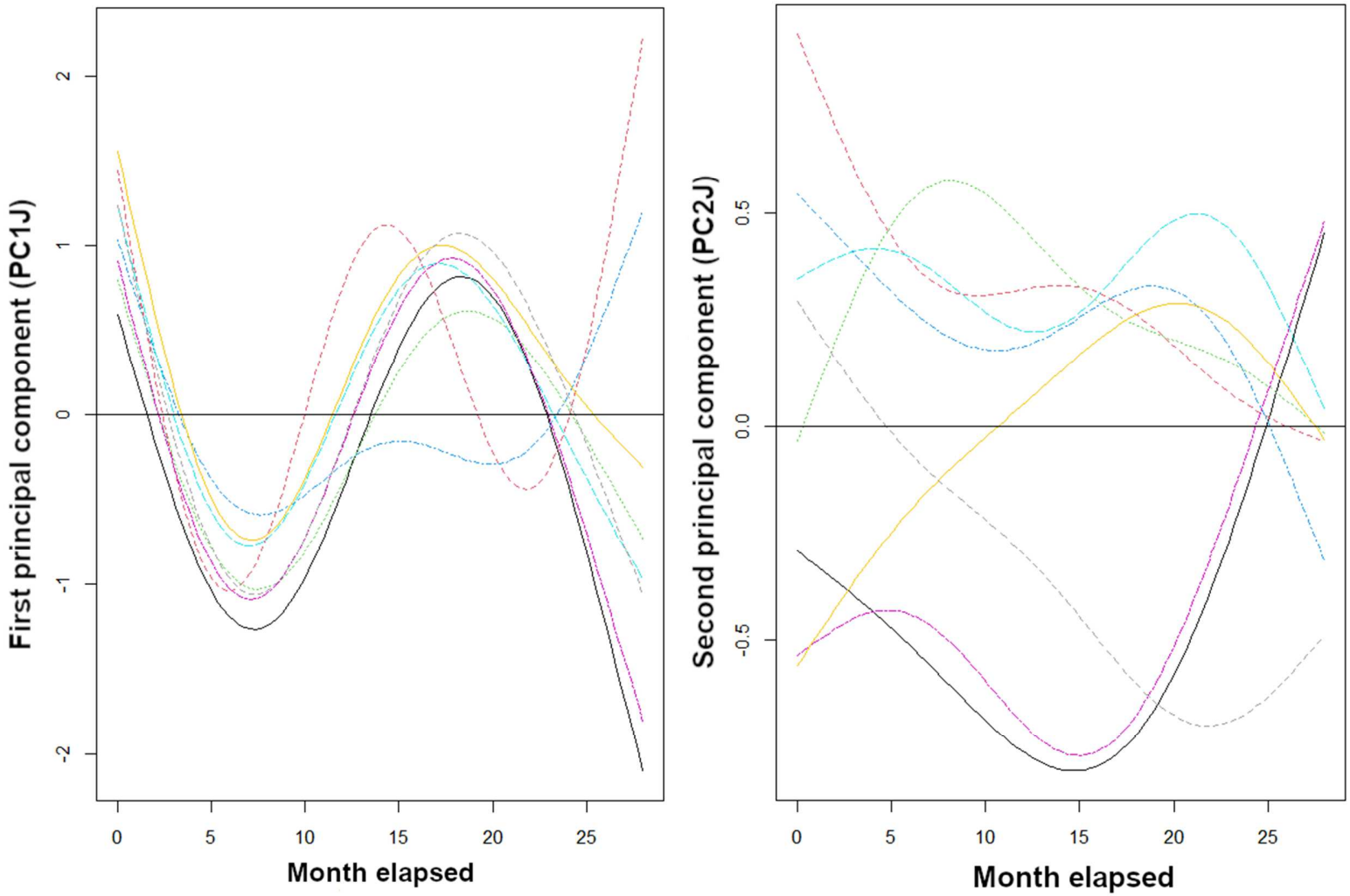

Figure S6 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs obtained using random intercepts and slopes (each coloured line representing an individual). Line corresponds to estimated smoother from the GAMM models

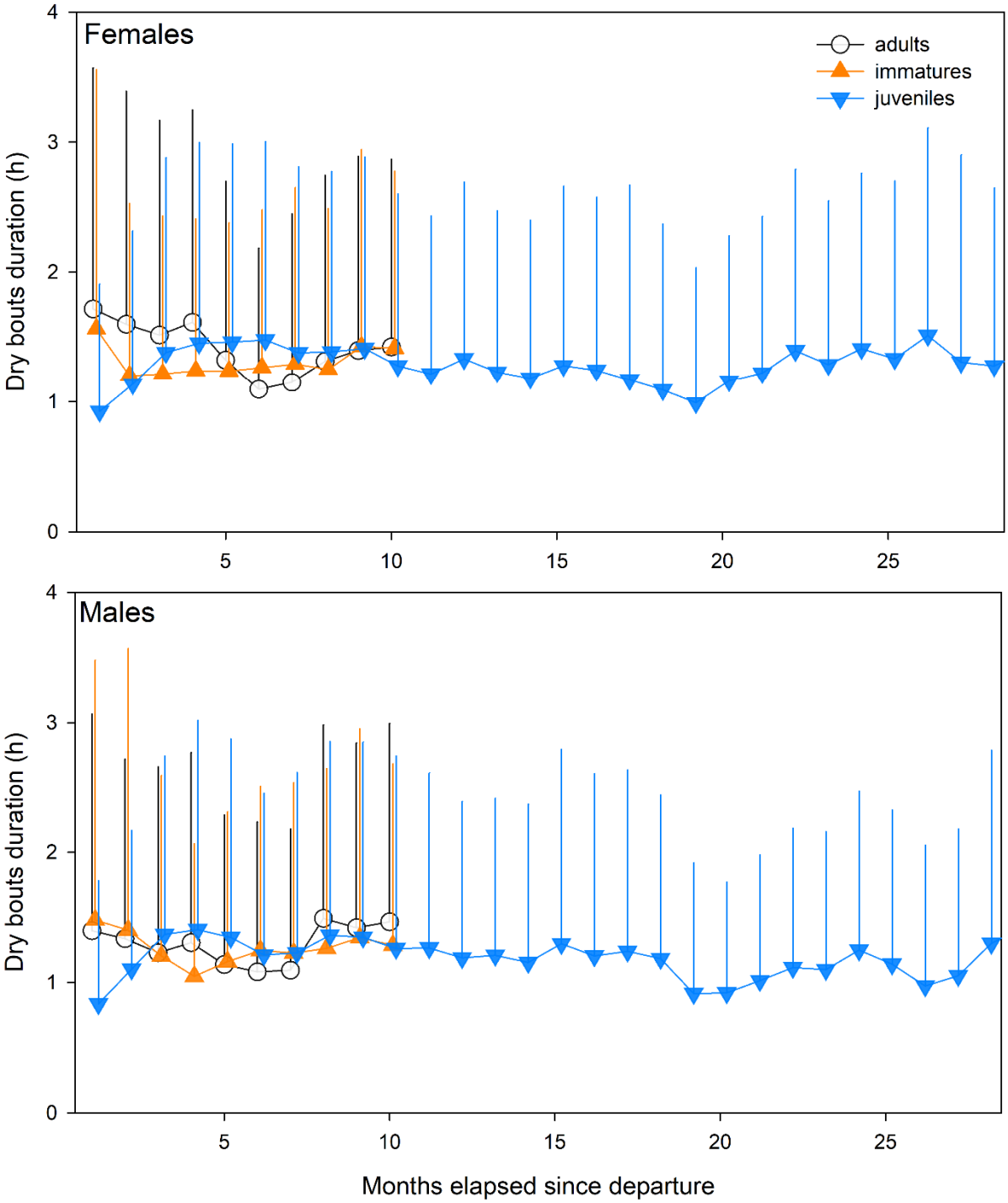

Figure S7 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

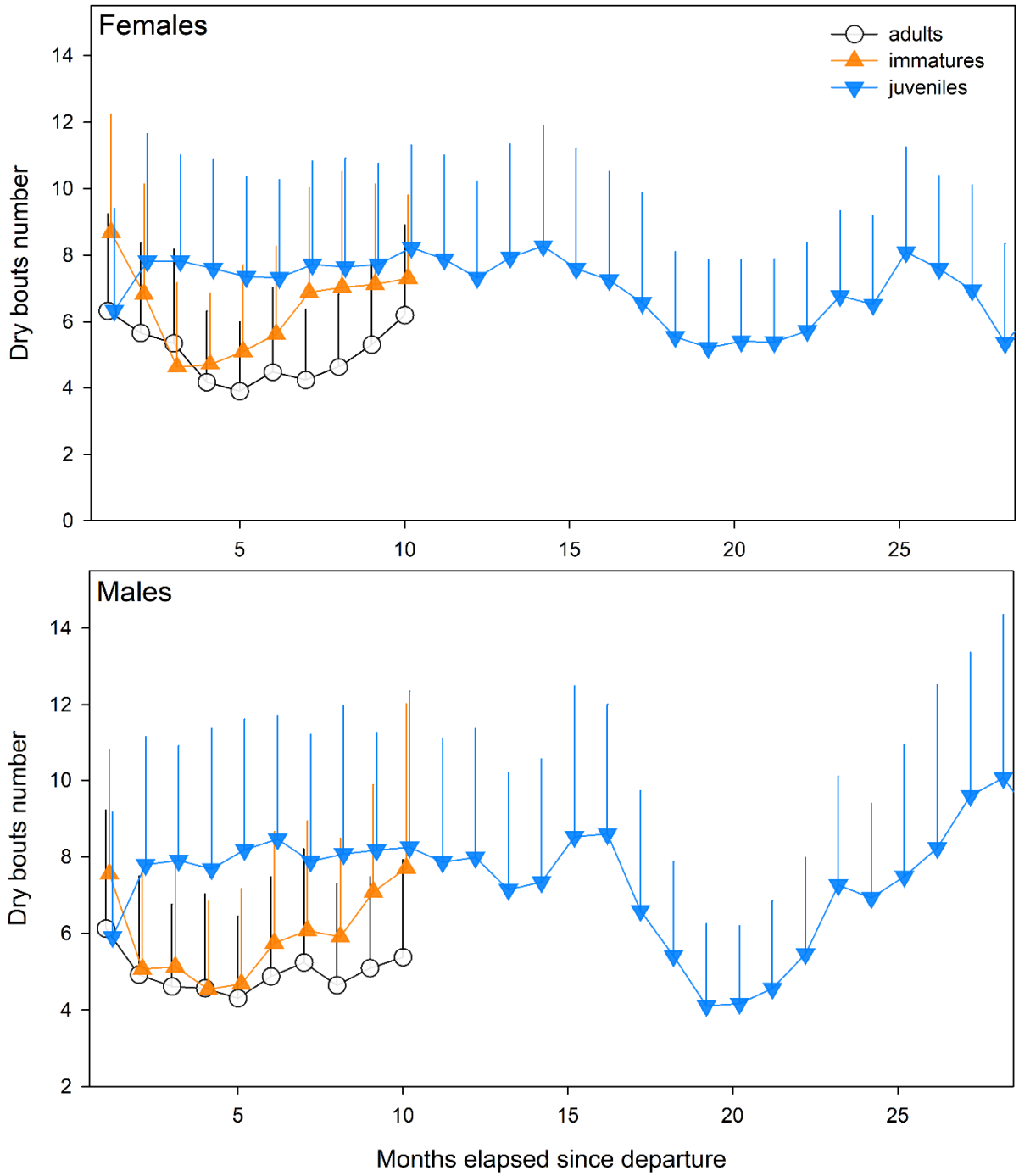

Figure S8 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

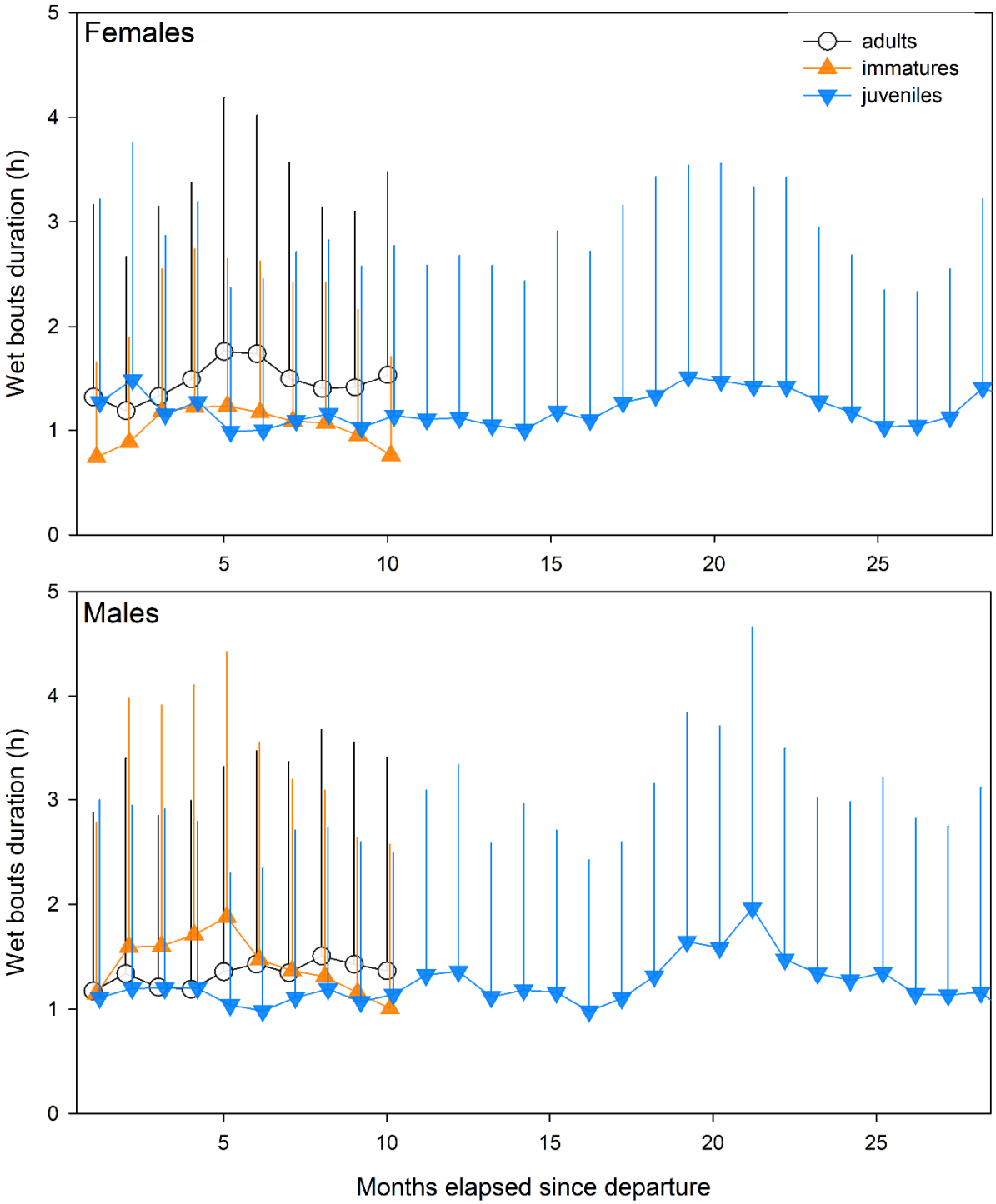

Figure S9 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

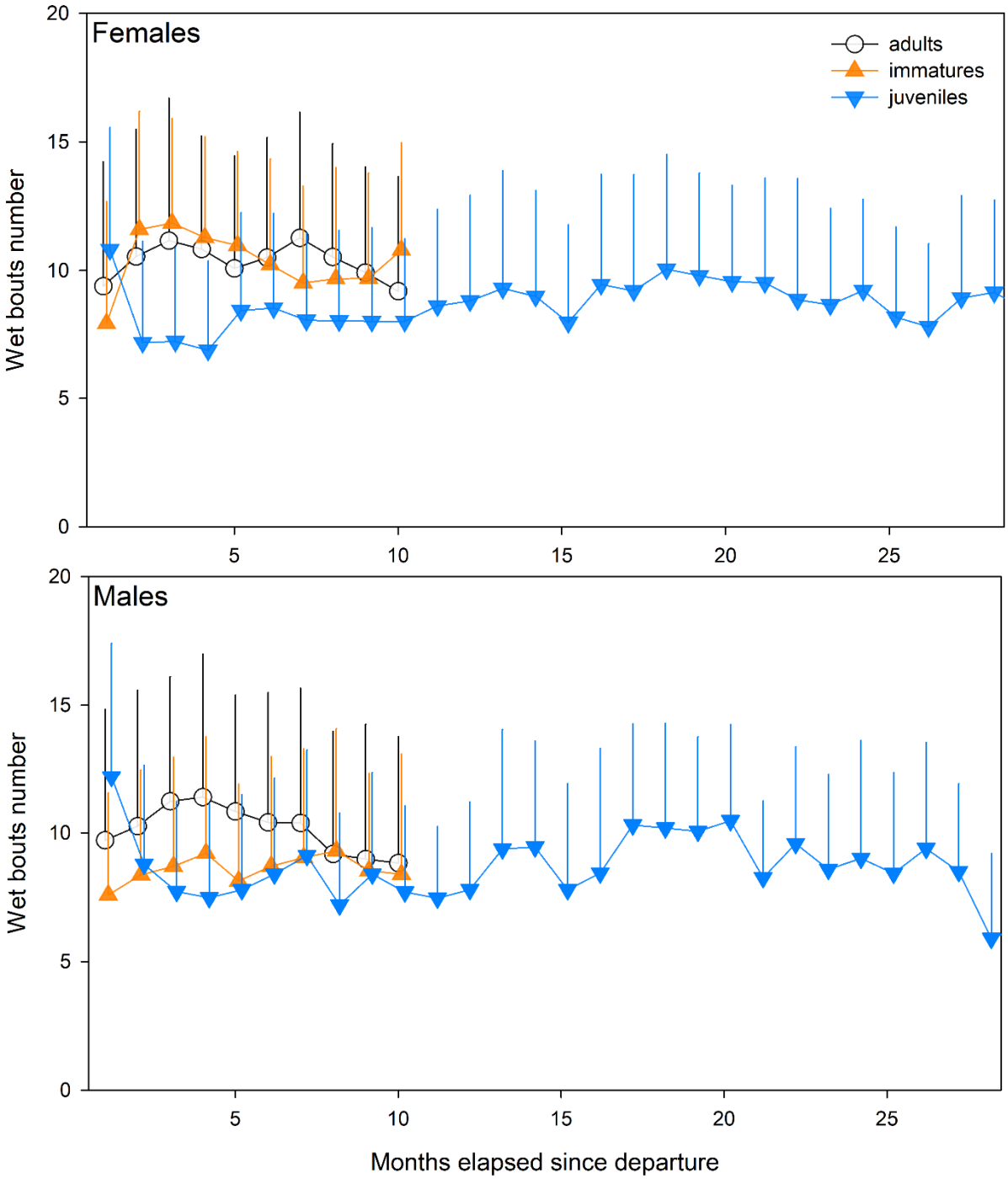

Figure S10 Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

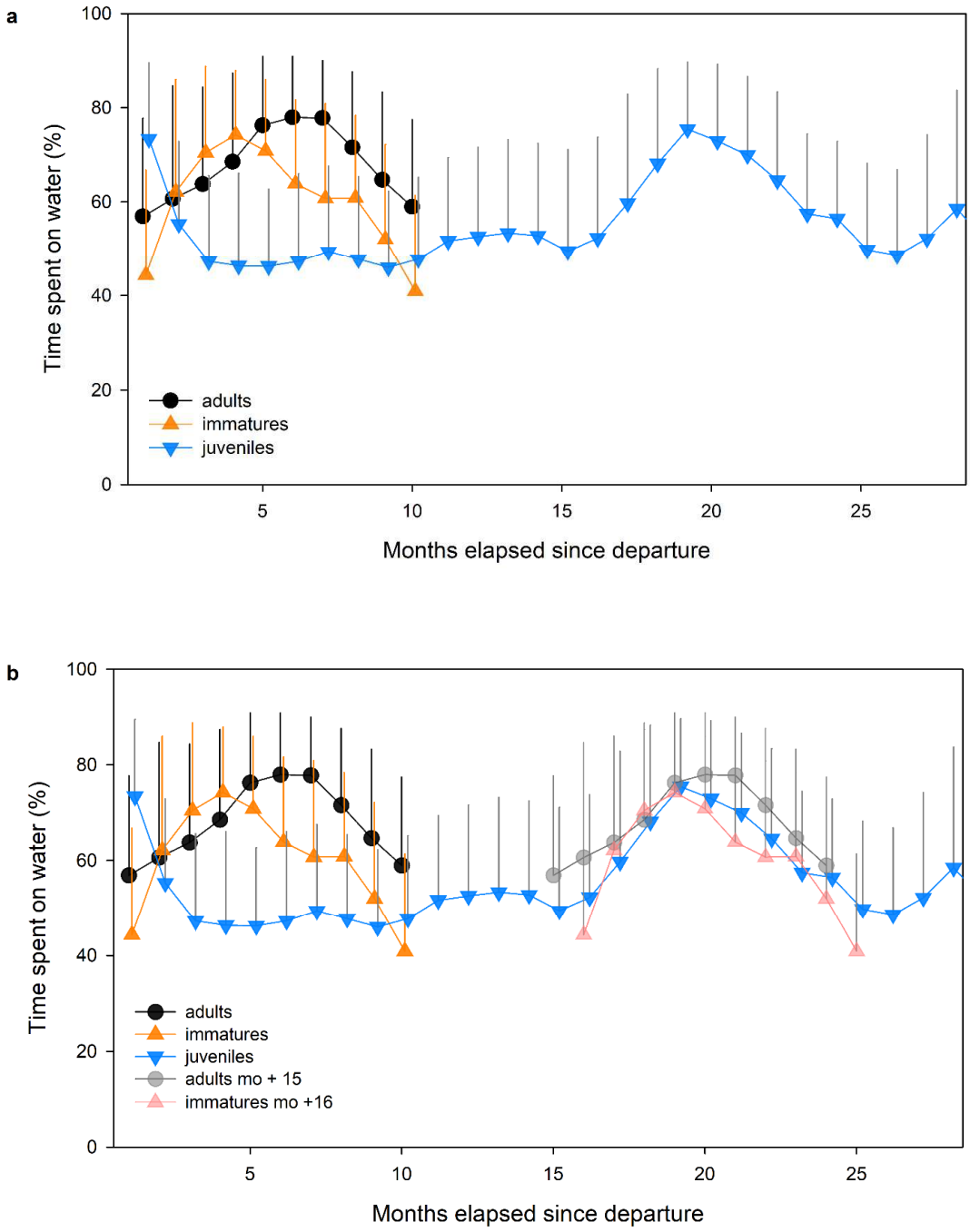

Figure S11 Daily proportions of time spent on water for every month since departure of the colony for juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel) and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel).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

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PCIEcology

Decision concerning your submission

Dear Karine Delord,

Your article, entitled **The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird**, has now been reviewed.

The referees' comments and the recommender's decision are shown below. As you can see, the recommender found your article very interesting but suggests certain revisions.

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

When revising your article, we remind you that your article must contain the following sections (see our Guide for Authors in the Help section of the PCIEcology website):

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- The "Data, script and code availability" section must clearly indicate **where and how** data can be accessed.
- Wherever possible, data, scripts and code should be provided in machine-readable formats. Avoid PDFs other than for textual supplementary information.
- Metadata should accompany the data, to make the data understandable and reusable by the reader.

2) **Supplementary information (if applicable)**

- Supplementary information (text, tables, figures, videos, etc.) can be referred to in the article. It must be available in an open repository (such as Zenodo, Dryad, OSF, Figshare, Morphobank, Morphosource, Github, MorphoMuseuM, Phenome10k, etc. or any institutional repository, etc...) with a DOI. A perennial URL can be provided if no DOI is available.

- A reference to the supplementary information, with a DOI or a perennial URL, must be provided in the reference list and in the "Supplementary information" section.
- List all documents attached to the manuscript as Supplementary Information in the "Supplementary Information" section.

3) **Funding (mandatory)**

- All sources of funding must be listed in a separate "Funding section". The absence of funding must be clearly indicated in this section.

4) **Conflict of interest disclosure (mandatory)**

- Authors should declare any potential non-financial conflict of interest (financial conflicts of interest are forbidden, see the PCI code of conduct).
- In the absence of competing interests, the authors should add the following sentence to the "Conflict of interest disclosure" section: "The authors declare they have no conflict of interest relating to the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is a recommender for PCI XX."

5) **Materials and methods (mandatory)**

- Details of experimental procedures and quantitative analyses must be made **fully available** to readers, in the text, as appendices, or as Supplementary Information deposited in an open repository, such as Zenodo, Dryad or institutional repositories with a DOI.
- For specimen-based studies, **complete repository information** should be provided and institutional abbreviations should be listed in a dedicated subsection (if applicable). Specimens on which conclusions are based **must be deposited in an accessible and permanent repository**.

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We thank you in advance for submitting your revised version.

Yours sincerely,

The Managing Board of PCIEcology

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

KARINE DELORD, HENRI WEIMERSKIRCH, CHRISTOPHE BARBRAUD

https://biorxiv.org/cgi/content/short/2021.10.23.465439v1 version v1
Submitted by Karine Delord 26 Oct 2021 07:51

Abstract

The transition to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher mortality including that of inadequate/inferior foraging skills compared to adults, young 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 #2

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by Blandine Doligez, 11 Dec 2022 23:02
Manuscript: **https://biorxiv.org/cgi/content/short/2021.10.23.465439v1** version v1

Revision needed

Dear authors,

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

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

- reduce the predictions at the end of the introduction to relate them to the first part of the section, i.e. focus on post-fledging learning while presenting more succinctly the need to account for other sources of changes in foraging behaviour (differences due to seasonal variations, molt or sex);

R: we reduced the predictions at the end of the Introduction and removed those specific to seasonal, moult of sex effects. We now explain that these factors were taken into account in the analyses focusing on the changes in foraging behaviour in juveniles. L112-135

Please notice that the line numbers mentioned in the answer refers to the revised version (R2, in track change mode).

- reduce the description of the species movements in the methods to what is necessary here (maybe more as a discussion when comparing different life stages);

R: the description of the species movements was reduced and partly moved to Supplementary. L182-200

- present the results of PCA in a table to avoid redundancy since the exact same variables are retained for the axes in both cases;

R: the results of PCA were removed from the Results section and are now synthetized in Table 3 in the revised version.

- reorganise the result section so as to make the test of predictions more apparent; for each section, start with changes with time elapsed and differences between stages, which correspond to the main objectives here;

R: we reorganised the paragraphs 'Changes in activity for all stages' and 'Changes in activity of juveniles during the first two years after fledging' accordingly, starting by presenting the select model, then the changes with time elapsed and finally differences between stages. L306-370

- reorganise tables and figures following the reviewer's suggestions to make them less numerous, clearer and more concise and avoid redundancy with the text.

R: we reorganised tables and figures according to comments (please see detailed answer below).

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

R: we considerably reduced this part of the discussions and merged the two paragraphs referring to time and sex effects in a single shorter paragraph. L451-527

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

R: following your comment we have now included in the GAMMs analysis the interaction between stage and time elapsed to formally test for gradual changes (Table 4). Interaction was significant for 1st and 2nd axes, this result was added (L311). We have moved and changed accordingly the Figure S6 (following reviewer comment; Figure 2 in the revised version).

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

- l. 669: the word dispersal may not be adequate here (movements instead?)

R: this was changed accordingly. L68

- l. 681-682: changes in behaviour

R: this was changed accordingly. L80-82

- l. 682: “when birds leave the colony…”: the timing is not very clear here (changes between what and what?). Please clarify.

R: this was rephrased. L80-82

- l. 687-688: given that behaviour is here studied through activity patterns, these two questions seem redundant. Maybe focus on differences between life-stages first and then changes within stages.

R: this was changed accordingly. L87-89

- l. 689-690: this remark is a bit strange here, maybe simply refer to the period during which instruments allow recording?

R: this sentence was added to answer to comments on longitudinality on round #1. The sentence was changed in the revised version to clarify. L89

- l. 697: “and increasing number and duration of flight bouts” (or rewrite for coherence)

R: this was changed accordingly. L98

- l. 698-699: not clear what “changes in activity following fledging” are and what they refer to later on in the study. Consider removing this part of the data (i.e. the fledging period), since it will of course be characterized by major changes but of no specific relevance here?

R: we reworded this part of the sentence which was not clear. L98-101

- l. 700: some capacities? what does this mean?

R: we now use performance rather than capacity which is more accurate and clearer. L103

- l. 794-797: I was a bit confused here as the information seemed contradictory (raw immersion data were obtained from testing every 3 s rather than 30 s; at first I thought that the maximum value could be 20 and not 200). Please rewrite.

R: this was rewritten to clarify. L204, 218-222

- l. 797-799: quite redundant, could be simplified.

R: this was simplified. L218-222

- a naïve question: how were GLS fixed on the birds? The corollary question being: when birds are sitting on water, does the GLS automatically get wet? I am wondering whether a distinction can be

made between a bird diving to catch food and a bird resting on sea (i.e. not flying), but is this distinction relevant here? (depending on the foraging biology of the birds)

R: the GLS were attached to a ring on the bird's leg, it is therefore unfortunately impossible to distinguish whether the animal is diving or not, for this it would be appropriate to use GLS that have pressure sensors (similar to time depth recorder).

- l. 812-814: please give the meaning of PTT and describe the method here – were PTT attached to GLS? not clear to me how this data was collected.

R: this was based on unpublished data obtained by deployment of Argos Platform Transmitters Terminals (PTT) on different birds and different years within another project. This was changed in the revised version. L235-243

- l. 873-876: not clear to me here; the issue of unbalanced sampling between sex and stage categories should not constrain a continuous size covariate? Please clarify.

R: the main reason why we did not include body size was due to small samples size. We reworded accordingly. L300-303

- Table 1: is dispersal again the right term for immatures here?

R: this was changed accordingly.

- Fig. 1 and 2: it would be good to add the raw data on the figures too, not just the model estimates.

R: figures were modified accordingly

- l. 944-946: a sentence very hard to follow, please rewrite (the "while… departure" part fo the sentence seems to be unconnected to the rest of the sentence).

R: this was rephrased in the revised version. L395-398

- l. 950: but when do we know whether juveniles exhibit similar behaviour to immatures or adults, if there is no formal test that the curves do not differ anymore after an initial period? (see main comment above). The comparison shown on fig. 12b is interesting, but should it not be statistically supported rather than remaining a simple visual comparison?

R: following your comment it is now tested formally (via interaction effect) and results were added in the revised version (Table 4).

Regarding the visual comparison shown in Figure S11 (in revised version), it is now statistically tested and differences remained between stages. A paragraph explaining the analysis was added in the Supplementary and the results shown in Table S4. We add a sentence on results in the main text (L409-410).

- l. 953-954: I do not think that the bell-shaped curve seen in months 15-16 after fledging suggest a behavioural change within the first two months. The sentence needs rewriting (at least, remove "together"?)

R: this was changed in the revised version. L406-407

- l. 956-958: any suggestion about what these changes may reflect, if not a change in performance?

R: these changes may reflect individual differences in used areas. Individuals may face different environmental conditions more of less favourable to obtain food resources or to mov due to differences in wind regimes. We added a sentence in the Discussion. L411-412

- l. 972-973: replace “lower performances” by “differences”

R: this was changed in the revised version. L427

- l. 980: “and that shortly after”: please rewrite

R: this was rephrased in the revised version. L434

- l. 988-990: any explanation for the difference between this species and others?

R: this could be due to differences in migration strategies but we feel this is likely too speculative to include a sentence here.

- l. 1011 and 1016: repetition “in seabird species”

R: this was changed in the revised version. L466-472

- l. 1027: remove “it”

R: this was changed in the revised version. L477-482

- l. 1040: rewrite (shorter what?)

R: this was changed in the revised version. L494

- l. 1048-1054: not clear here which sex is concerned. Consider rewriting for clarity (or delete since this is not the main question of interest – see main comments)

R: this paragraph was removed as explained above. L498-516

- l. 1057: more subtle than what?

R: this paragraph was removed as explained above.

- l. 1060-1062: seems largely out of scope here (differences between species, which ones?): delete?

R: this was deleted in the revised version.

- The conclusion, being merely a summary here, does not seem needed as it does not bring any additional thought here and simply repeats the main results again.

R: I am a bit confused here, because the conclusion paragraph was added following the reviewer comment on round #1. Nevertheless, if you still consider it unnecessary we will be happy to delete it.

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

- l. 632 : remove final parenthesis

R: done. L30

- l. 643: hypothesis

R: done. L41

- l. 687: behave

R: done. L87

- l. 689: do

R: done. L89

- l. 699: wandering albatross fledglings

R: done. L101

- l. 772: replace by “secondly” or “in a second step”?

R: done. L195

- l. 773: “juvenile and adult patterns” or “patterns for juveniles and adults”

R: done, removed.

- l. 798: the proportion of time

R: done. L222

- l. 849: variables

R: done. L276

- l. 849: we ran separate models

R: done. L276

- l. 870: measurement (or “each of the…”)

R: done. L297

- l. 882: in the Amsterdam albatross (or albatrosses)

R: done. L307

- l. 896: add a comma after departure

R: done. L335

- l. 906 (see also l. 1129): juvenile Amsterdam albatrosses or Amsterdam albatross juveniles

R: done. L313

- l. 907: for all three activity variables considered – also specify more clearly that the sex effect was found only for PC2 and PC3.

R: this was rephrased in the revised version. L313-315

- l. 967: delete "among"

R: done. L421

- l. 969: the same

R: done.

- l. 1057: "some a trade-offs in duration and numbers": clearly needs rewriting!

R: this was rewritten in the revised version.

- l. 1071: female Amsterdam albatrosses or Amsterdam albatross females

R: done.

- l. 1121 and 1129: variation in activity…

R: done.

- l. 1158: i.e. instead of e.g

R: done.

Review of Delord et al., "The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird", Revision 1

I appreciated the chance to review the revised version of this paper and apologize for the delay in providing my review.

I was impressed by the extensive work that went into this revision. Overall, the analytical changes made by the authors largely address my concerns related to the analysis itself. The PCA approach is a helpful way of condensing the different wet/dry variables while revealing some of the tradeoffs between them (e.g., duration vs. number of wet bouts). Meanwhile, the GAMMs account for among-individual variation and allow for continuous temporal processes, which makes the results clearer to interpret. The analysis in its current form generally seems sound.

However, I still experienced some confusion in contextualizing and interpreting the results, and had to read through the paper a few times to fully grasp them. I think this stems from the fact that the results and discussion aren't always linked back clearly to the hypotheses presented at the start of the paper. The PCA adds an extra layer of complication since one has to remember in some cases what each of

the synthetic variables represent. I think this issue could be solved by some condensing and re-framing, particularly in the Introduction/Methods, as well as some thought to data depiction, particularly adding partial effects plots to more clearly show the contrasting effects of time, seasonality, and sex across different life stages. My overall suggestion would be to refer back to the hypotheses in structuring the results, tables/figures, and discussion. This would help the reader clearly link the findings of the paper with the ecology of the species and the authors' initial predictions.
R: thank you for very enthusiast and positive comments

Comments on the tables/figures
Tables 1-2: These two tables could potentially be combined to show definitions, sample sizes, and tracking durations for each group. Some of the information in Table 1 (particularly definitions and behavior) repeats information in the text and could be condensed.
R: the two tables were combined and information condensed in Table 1 in revised version

Tables 3 & 5: I might suggest rearranging these so that the models are shown from lowest to highest AIC scores, and calculating Δ AIC values compared to the top model rather than the null. This makes it easier to see which model(s) received the most support and compare against other tested models.
R: these tables was revised accordingly

Tables 7-12: I would suggest combining these into a single table and making it a supplementary table (since these comparisons are also covered in Table 6). Although measuring dimporphism is important and relevant, I'm not sure it's the main contribution of this study, and it seems overrepresented in the tables.
R: as suggested we combine Tables 7-12 in two tables and moved in the supplementary (Tables S5-S6)

Figures 1-2: I think these figures present a useful contrast and appreciate that the authors listed the primary contributing variables on the Y-axis for each. It might also be helpful to briefly re-state in the caption what the primary variables were that structured each axis.
R: brief information on variables structuring the 1st and 2nd was added in the caption accordingly

Additional figure/table suggestions:
Table S1: This table is very helpful, and I found myself referring to it a lot while reading. I might suggest making this part of the main document and minimizing as much as possible the description of the hypotheses in-text, since I found the table very easy and straightforward to interpret. References supporting each hypothesis could be incorporated into the table itself if needed. It also seems notable that the three columns in this table correspond approximately to the three principal components. I wonder if there is a way to make this clearer in the table and/or in the text of the article, since it will make interpretation of the results more straightforward if the reader can refer directly to this table to see how a given predictor was expected to behave and compare that with how it actually behaved. In general, creating clearer links from these hypotheses to the results and subsequent discussion would help to structure the flow of information. One minor point/question: I am not sure why a two-period activity schedule is assumed for adults (reduced activity during molt?). There seems to be some overlap between B and C. It might be simpler to confine Hypothesis C to seasonal effects (i.e., external environmental change) and Hypothesis B to molt/energetic effects (i.e., internal requirements), assuming that's appropriate.
R: we thank the reviewer for this very positive comment on this Table S1 which was initially in the main manuscript and which has been moved following previous comments and suggestions. This table was moved accordingly in the main manuscript (Table 1) and changed following your comments and the Editor's comments.
To answer to your question regarding the two-period schedule, yes, it is assumed a reduced activity during moult based on what have been evidenced on other species of albatross, due to possible impairment of flying ability.

Figure S6: This is also very useful and could be a main figure, since it directly shows the contrast between adults, immatures, and juveniles. Indeed, Figure S6 seems to directly correspond to Hypothesis A in Table 1. It would be great to add the main loading variables to the Y axis (as in Figures 1-2) and potentially add subfigures for PC2 and PC3, since the principal components correspond approximately to the three columns in Table S1. If possible, it would also be helpful to consider including additional figures corresponding to the other hypotheses (potentially partial effects plots for the corresponding covariates in the GAMMs) to make it easy for the reader to see which hypotheses were supported and where the study might have diverged from expectations.
R: following your suggestions Figure S6 was modified and included in the main manuscript (Figure 2). We add sub figures for PC2 and PC3 as suggested. Following the Editor's comments, we simplified the hypotheses and removed C) Seasonal environmental change and D) Sex-specific body size, and they are now considered as co-factors.

Comments on the text:
Lines 691-727: This section could be considerably reduced and some of the information and references moved to Table S1.
R: this section was largely shortened and reorganized in the revised version following reviewers' comments.

Study Species and Data Loggers section (Lines 730-): This contains a lot of background information interspersed with methods, making it a bit hard to follow. I'd suggest focusing this section more explicitly on the methodology, with information on the species presented as necessary at the start of the section to define life stages.
R: following your comments, background information was shortened and referred to Supplementary.

Lines 733-744 and 751-776: More like background information; duplicated in Supplement – delete?
R: following your comments, background information was shortened and referred to Supplementary.

Lines 832-845: Information on the principal components and variable loadings could be summarized in a table to reduce text and allow for easy reference.
R: this has been changed accordingly in the revised version.

Lines 869-873: Explain why both T-tests and GLMs are needed?
R: GLMs tested for effect of sex and stage and T-tests tested the differences of body size measurements between males and females. This was added in the Methods Section. L300

Line 839: "components"
R: changed

Line 877: Missing "R" before citation.
R: changed

Results: I would suggest reorganizing this section to match the hypotheses. Lines 882-887 (and 906-911?) could be presented as an introductory paragraph, followed by separate paragraphs discussing differences among stages, specific effects of time since departure, month/season (and differences among stages), and sex-specific effects, with a figure illustrating each paragraph.
R: this section was reorganized according to the Editor's comments

Line 906: "juvenile Amsterdam albatrosses"
R: changed

Line 918: This pattern is visible in Figure S6 (another reason it might be useful as a main figure!)
R: changed, please see my above answer

Lines 936-939: This could be rephrased to focus on what the study did do (rather than what it didn't do). Something like "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."
R: this was modified according to your suggestion.

Lines 949-951: It might be helpful to show the equivalent of Figure S6 for PC2 and PC3 to illustrate this increasing similarity.
R: following your suggestions Figure S6 was modified as suggested (Figure 2).

Lines 951-953: I wonder if it would be useful to present a comparison of juvenile behavior lagged by 1 year with non-lagged juvenile, adult, and immature behavior, to help illustrate the increasing similarity to other life stages while controlling for seasonality? Not sure if this is helpful; just a thought.
R: following Editor's comment we added gamm analysis taking into account a time lag. Figure S11 (in revised version), it is now statistically tested and differences remained between stages. A paragraph explaining the analysis was added in the Supplementary and the results shown in Table S4. We add a sentence on results in the main text (L409-410).

Line 989: Should be "to rapidly fly"
R: changed

Line 997: Make section heading consistent with Table S1?
R: changed

Lines 998-1002: Would suggest removing this sentence (repeats previous section) and focusing exclusively on seasonal/environmental changes across all groups.
R: this was modified according to Editor's comments

Line 999: Should be "juvenile Amsterdam albatrosses"
R: changed

Line 1000: "more adult-like behavior"
R: changed

Lines 1007-1010: Were there any specific behavioral changes during the austral winter that might be linked to this seasonal change in productivity? Partial effects plots for the GAMMs showing the effect of month might be a helpful reference here for complex/non-linear changes.
R: Yes indeed changes occurred in behaviour according to months of the year, as initially illustrated (V1; Figures 1-5) but removed following reviewers comments. This paragraph was modified according to Editor's comments.

Lines 1011-1017: I'm not sure if this is relevant, since the reproductive period was not included in this study. If the results of this study show evidence of carry-over effects in sabbatical adults, then it would be helpful to make that case here. Otherwise, I'd suggest deleting this paragraph.
R: this was removed in the revised version following Editor's comments.

Lines 1018-1032: Largely repeated in the Supplement – delete?
R: this was shortened accordingly.

Line 1034: I would suggest making subheading titles and hypotheses consistent (e.g., use "Sex differences in activity" as the title for Hypothesis D)
R: this was modified in the revised version following Editor's comments.

Line 1038: The "body-size hypothesis" is mentioned here, but not explained earlier—I assume this is a relic of the previous version? Perhaps rephrase. I'm also not sure it makes sense to refer to this as a body size effect, since the sample was not sufficient to separate effects of body size from those of sex and sex is essentially used here as a proxy for body size. Even in non-dimorphic species, sexes sometimes behave differently, which suggests that behavioral differences could be related to sex-specific energetic requirements or physiology. It would be more accurate to say that the sexes differed, with a likely driver of that difference being dimorphism and concomitant effects on wing-loading.
R: this was removed in the revised version
Line 1046: Missing parenthesis.
R: changed in the revised version

Lines 1044-1054: I might suggest moving some or all of this section to the supplement, to focus more clearly on the results of this study and how they did or didn't support the hypothesis already described.
R: this was removed in the revised version

Lines 1063-1073: This paragraph provides context on the influences of body size and wing-loading that would have been useful before the previous paragraph—perhaps swap these two paragraphs? R: this was reorganized in the revised version

Lines 1082-1085: This is really interesting !
R: thank you