## TITLE

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

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

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

## Abstract

The transition to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher mortality including that of inadequate/inferior foraging skills compared to adults, young naïve individuals combining lack of experience and physical immaturity. Thus a change in behaviour, resulting in an improvement of skills acquired from growing experience, is expected to occur during a period of learning through the immaturity phase. Very few studies have investigated the ontogeny of foraging behaviour over long periods of time, particularly in long-lived pelagic seabirds, due to the difficulty of obtaining individual tracking data over several years. We investigated the foraging behaviour, through activity patterns, during the three life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naïve juveniles, immatures and adults. Naïve juveniles during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, longer and more numerous bouts on water, shorter and fewer flying bouts). Patterns of activity parameters in juveniles after independence suggested a progressive change of foraging performances during the first two months 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*

35

## 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.

GLS are archival light-recording loggers used to study activity of birds over periods lasting up to ~ 2 years. GLSs record the ambient light level every 10 min, from which local sunrise and sunset hours can be inferred to estimate location every 12 h (Wilson et al. 1992). GLS also recorded saltwater immersion data by testing for saltwater immersion at regular interval, storing the number of samples wet (>0) at the end of each 10 min period. We used saltwater immersion to estimate daily activity budget. Despite the higher mean spatial error of location estimates with these devices (over 100 km; Phillips et al. (2004a)), GLS loggers allowed us to track the birds for prolonged periods with minimal disturbance to them. We considered the following stages regarding the year of GLS deployment (see Table 1): juvenile, as a fledgling equipped with a GLS just before leaving the colony for the first time; immature, as a non-breeding young bird that had never bred equipped with a GLS when visiting the colony; adult, as a breeding adult equipped with a GLS during the incubation or brooding period which successfully fledged a chick and thereafter took a sabbatical year. To date, we have retrieved 40 of the 50 GLS loggers deployed in total over 4 years, from which 33 individual tracks were estimated (Table 1). Our original aim was to collect activity data over the three life-stages on a long period of time (>1 year). These data are available from a total of 10 adults tracked throughout their sabbatical period, 13 immature birds and 10 juvenile birds (up to 3.2 years).

## Data processing

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

To select the data corresponding to periods spent at sea after leaving the breeding site, we used the following criteria on activity to define the departure time from the colony for each stage: 1) juveniles, the first bout spent on seawater (wet bouts duration) > 1h based on 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 on water and time spent on water, wet bouts duration and dry bouts duration, wet bouts number and dry bouts number) and to avoid redundancy, we ran principal components analyses (PCA built with the 'PCA' function, FactoMineR package (Lê et al. 2008)) to circumvent collinearity issues. To describe behaviours using gradients of activity we ran PCA for i) all stages (PCS; based on activity data collected during the first ten months post-departure) and for ii) juveniles only, as an additional goal was to determine changes in activity patterns during the first two years of life (PCJ; based on activity data collected during the first twenty-nine months post-departure).

Considering all stages, the first three principal components (PCS) explained 94.2% of the total variance. For juveniles, the first three principal components (PCJ) explained 92.2% of the total variance. The detailed results of PCA and the variables retained for each axe are summarised in Table 3.

Second, we used generalized additive mixed models (GAMMs, built with the 'gam' function, itsadug and mgcv package, (Lin and Zhang 1999; Wood 2015)) with the values associated with each of the three first axes of the PCA as the dependent variables. We ran separate models testing for variability in activity parameters i) for all stages combined (PCS) and ii) for juveniles (PCJ), based on different duration of datasets (28 months since departure for juveniles and 9 months since departure for immatures and adults; see Supplementary; Table S1). Thus, for i) we considered the lowest number of months elapsed since departure available (9 months since departure). Months elapsed since departure (the duration elapsed since fledging expressed in month, i.e. the first month after fledging and so on), month of the year (i.e. January and so on), sex, and stage (only for i)) were included as fixed effects. To test for the importance of individual variability in our results we built models with or without random effects. We compared models without random effect, models with random intercepts, and models with random slopes and intercepts to test whether the rate of change of activity parameters as a function of time elapsed since departure varied between individuals (Zuur 2009a). Models included month elapsed since departure as a continuous covariate modelled with non-parametric smoothing functions (Wood 2017). We limited the amount of smoothing (k) with the 'gam.check' function following Wood (2017) for each spline to avoid excessive flexibility and model overfitting that would have no ecological meaning. Models including all combinations of explanatory variables and random effects were then tested and ranked using their Akaike Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach (Burnham and Anderson 2002). The model with the lowest AIC was considered as the best model. Two models separated by a difference in AIC values of less than 2 were assumed to fit the data similarly.

### *Variation in body size*

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

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

## **Results**

The most parsimonious models explaining variations in activity parameters in the Amsterdam albatross included time elapsed since departure from the colony, month of the year, stages and sexes (Tables 4 and 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.

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

[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

Table 2 Hypotheses and predictions about the factors driving differences in activity (time spent on water, number and duration of flying bouts, number and duration of water bouts) year-round in Amsterdam albatrosses

| | Predictions | | |
|---|---|---|---|
| Hypothesis | Time spent on water (%) | Flying bouts (number/duration) | Water bouts (number/duration) |
| (A) Age and stage specific | Juveniles: increased foraging time/effort and thus lower time spent on water than other stages | Juveniles: increased foraging time/effort and thus longer flying bouts than other stages | Juveniles: increased foraging time/effort and thus shorter water bouts than other stages |
| (B) Temporal changes - internal requirements: moult/energetic effects | Adults/immatures: two-periods pattern including one with lowering activity<br>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<br>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<br>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<br>Higher time spent on water during moulting | Adjustment in foraging effort to energetic requirements or moult constraints according to time elapsed since departure<br>Lower flying bouts duration and number during moulting | Adjustment in foraging effort to energetic requirements or moult constraints according to time elapsed since departure<br>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 |

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**<br>**P<0.01** | **$t_{64}$=-4.882**<br>**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**<br>**p<0.001** | **$t_{28}$= -3.982**<br>**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**<br>**p<0.001** | **$t_{72}$= -4.268**<br>**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**<br>**p<0.001** | **$t_{58}$= -4.821**<br>**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**<br>**p<0.001** | $t_{32}$=0.512<br>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)

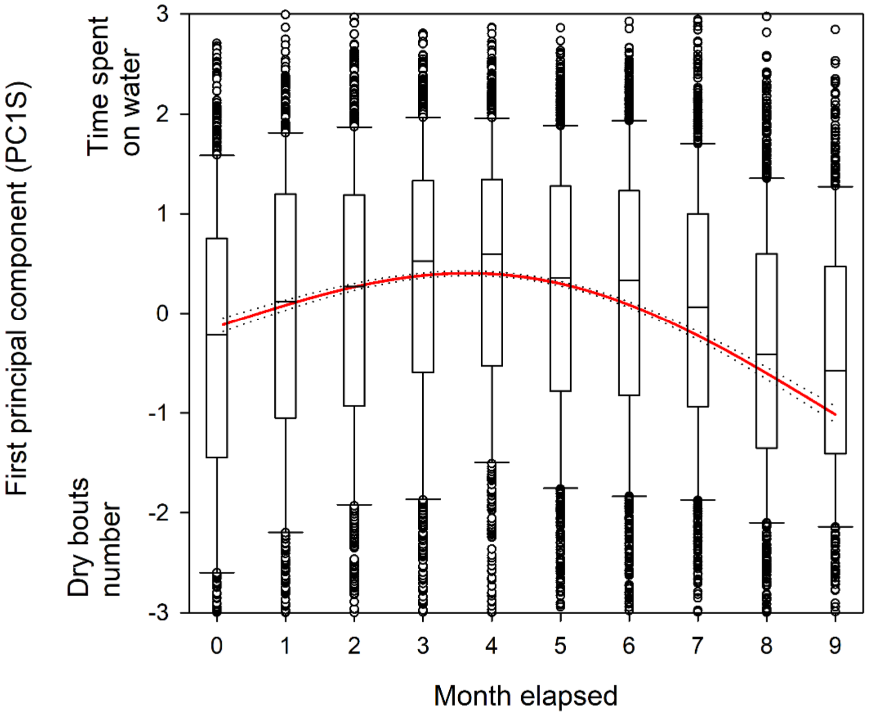
## FIGURES

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

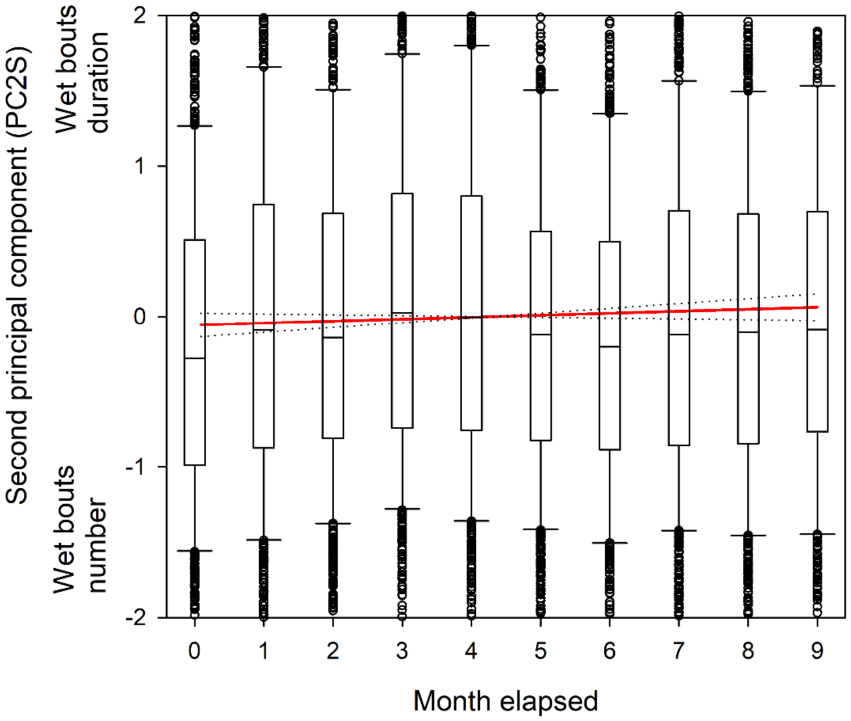
Figure 3 Modeled a) first and b) second axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Plain line corresponds to estimated smoother from the GAMM model.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

501 Figure 1a



502

503 Figure 1b



504

Figure 2a

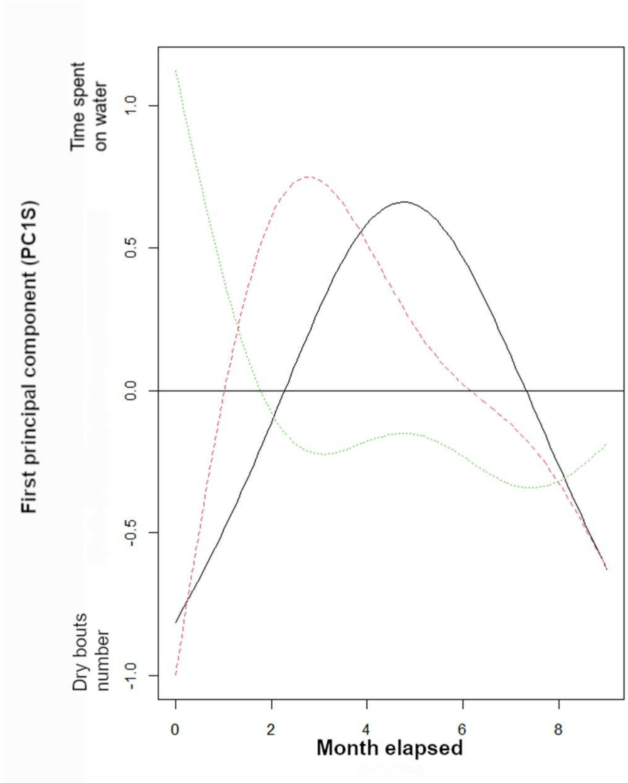


Figure 2b

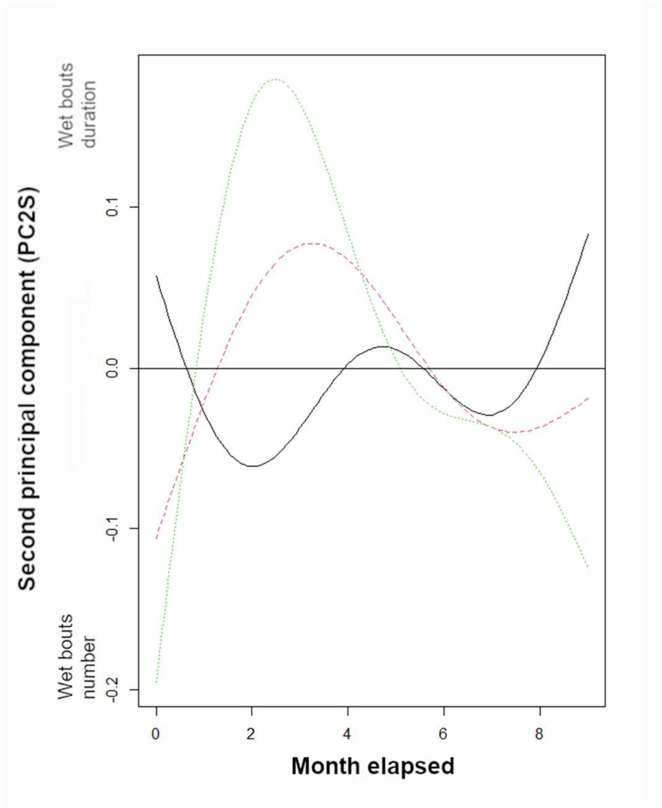


Figure 2c

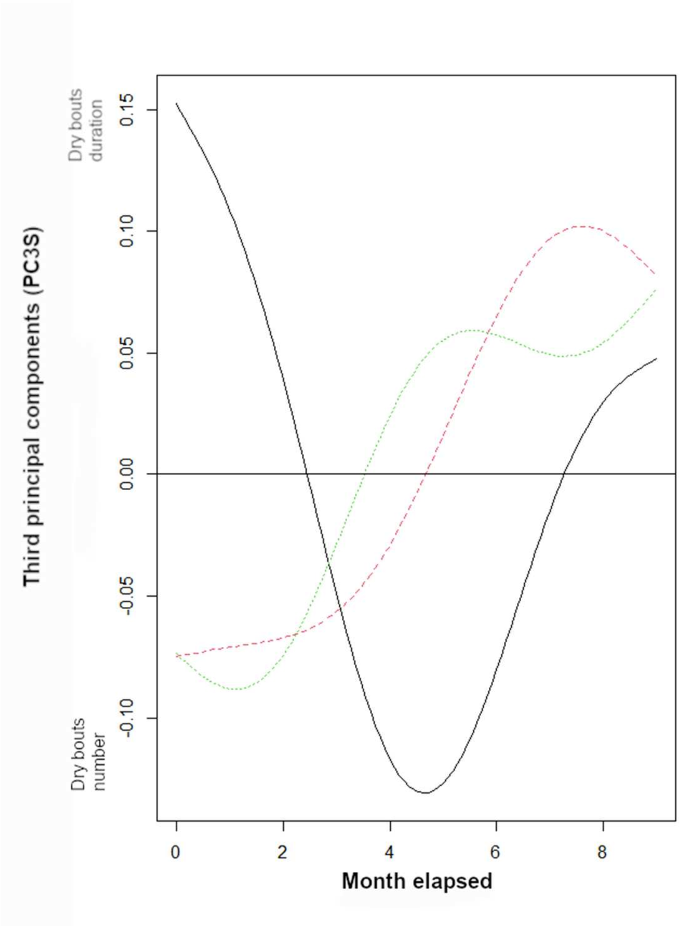

Third principal components (PC3S)
Dry bouts duration
Dry bouts number
0.15
0.10
0.05
0.00
-0.05
-0.10
0
2
4
6
8
Month elapsed

Figure 2a

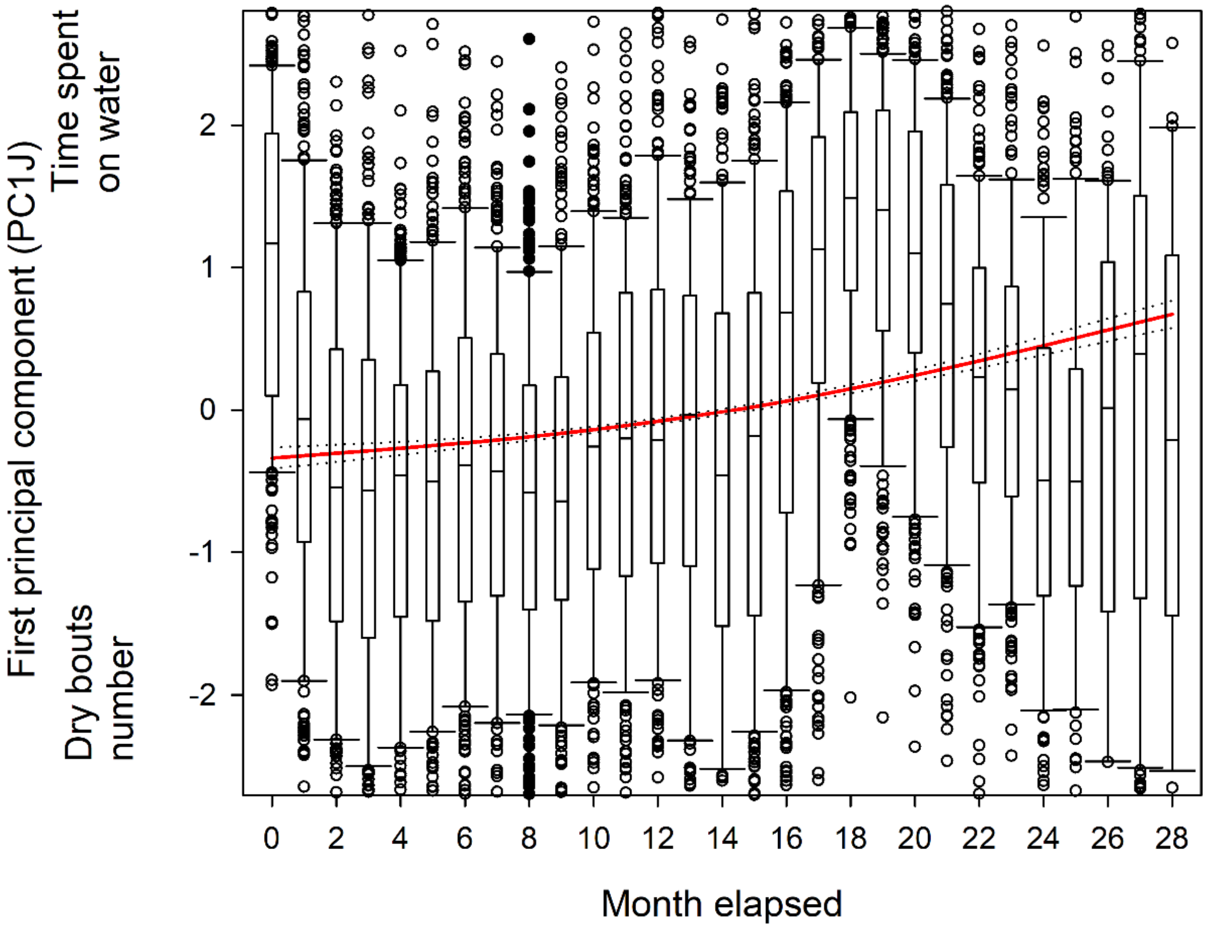
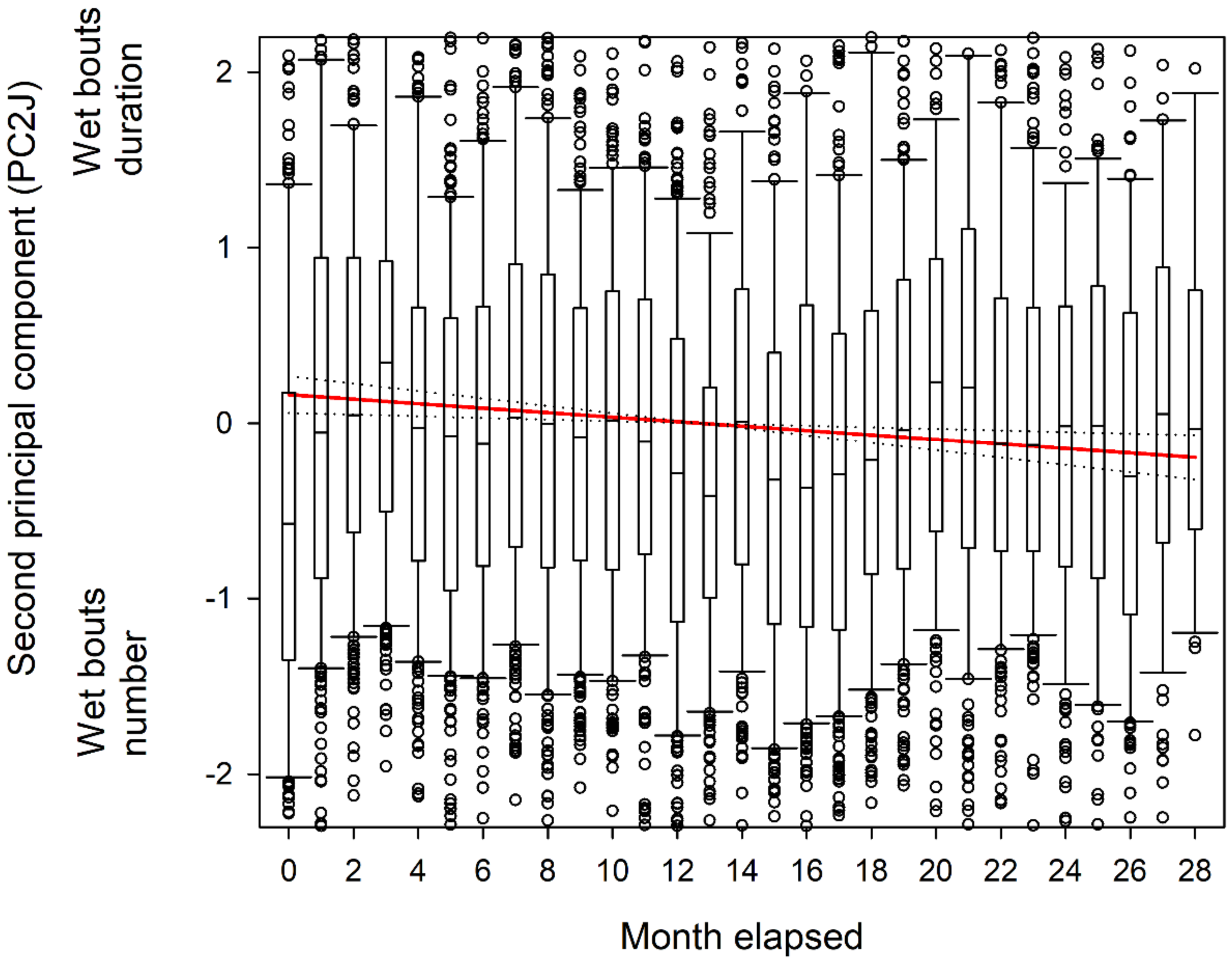

Time spent on water
First principal component (PC1.J)
Dry bouts number
2
1
0
-1
-2
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Month elapsed

Figure 2b



Wet bouts duration
Second principal component (PC2J)
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.**

## REFERENCES

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

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

Barbraud C, Delord K, Kato A, et al (2019) Sexual segregation in a highly pagophilic and sexually dimorphic marine predator. bioRxiv 472431, ver. 4 peer-reviewed and recommended by PCI Ecology (2019). Doi.org/10.1101/472431

Becker J (2014) Dispersal and Genetic Variation in a Naturally Fragmented Environment: Insights from a Long-term Study of White-throated Dippers (Cinclus cinclus)

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

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

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

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

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

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

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

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

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

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

Corbeau A, Prudor A, Kato A, Weimerskirch H (2020a) Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. Journal of Animal Ecology 89:20–28

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

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

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

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

Delord K, Barbraud C, Bost CA, et al (2013) Atlas of top predators from the French Southern Territories in the Southern Indian Ocean. http://www.cebc.cnrs.fr/ecomm/Fr_ecomm/ecomm_ecor_OI1.htm. DOI 10.15474/AtlasTopPredatorsOI_CEBC. CNRS_Territoires australs français l

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

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

Evans DR (2018) The post-fledging survival and movements of juvenile Barn Swallows (Hirundo rustica): an automated telemetry approach

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

Frankish CK, Manica A, Clay TA, et al (2022) Ontogeny of movement patterns and habitat selection in juvenile albatrosses. Oikos 2022 (6). e09057

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Weimerskirch H, Delord K, Guitteaud A, et al (2015a) Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Scientific Reports 5(1): 8853

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

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

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

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

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

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

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

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

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

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

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

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

## Supplementary

### Species biological aspects

Though the diet and foraging strategy of Amsterdam albatross remains poorly known, it is presumed to have very similar foraging behaviour compared to that of the wandering albatross, although subtle differences can appear (Pajot et al. 2021). Like other large albatross species (*Diomedea spp.*), the Amsterdam albatross is likely to prey on large squid, fish and carrion found on the sea surface (Delord et al. 2013, Cherel et al. unpublished data). The wandering albatross is known to forage over extensive distances, detecting prey visually or by olfaction during the day (Nevitt et al. 2008). This strategy referred as '*foraging-in-flight*' is the lowest energy consuming feeding strategy for the wandering albatross (Weimerskirch et al. 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.

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

| | **Model #** | **Study variable**[1] | **Model structure** | **Sample size** |
|---|---|---|---|---|
| All stages | gamm1 | PC1S | ~s(monthelap, 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 |

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

Table 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 |

Table S2b GAMM results for the second principal components (PC2S; gamm2 see Table S2) of Amsterdam albatross modelled as a function of months spent since departure from the colony (monthelap), month of the year, stage and sex. Reference values are January, adults and females.

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

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

Table 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**

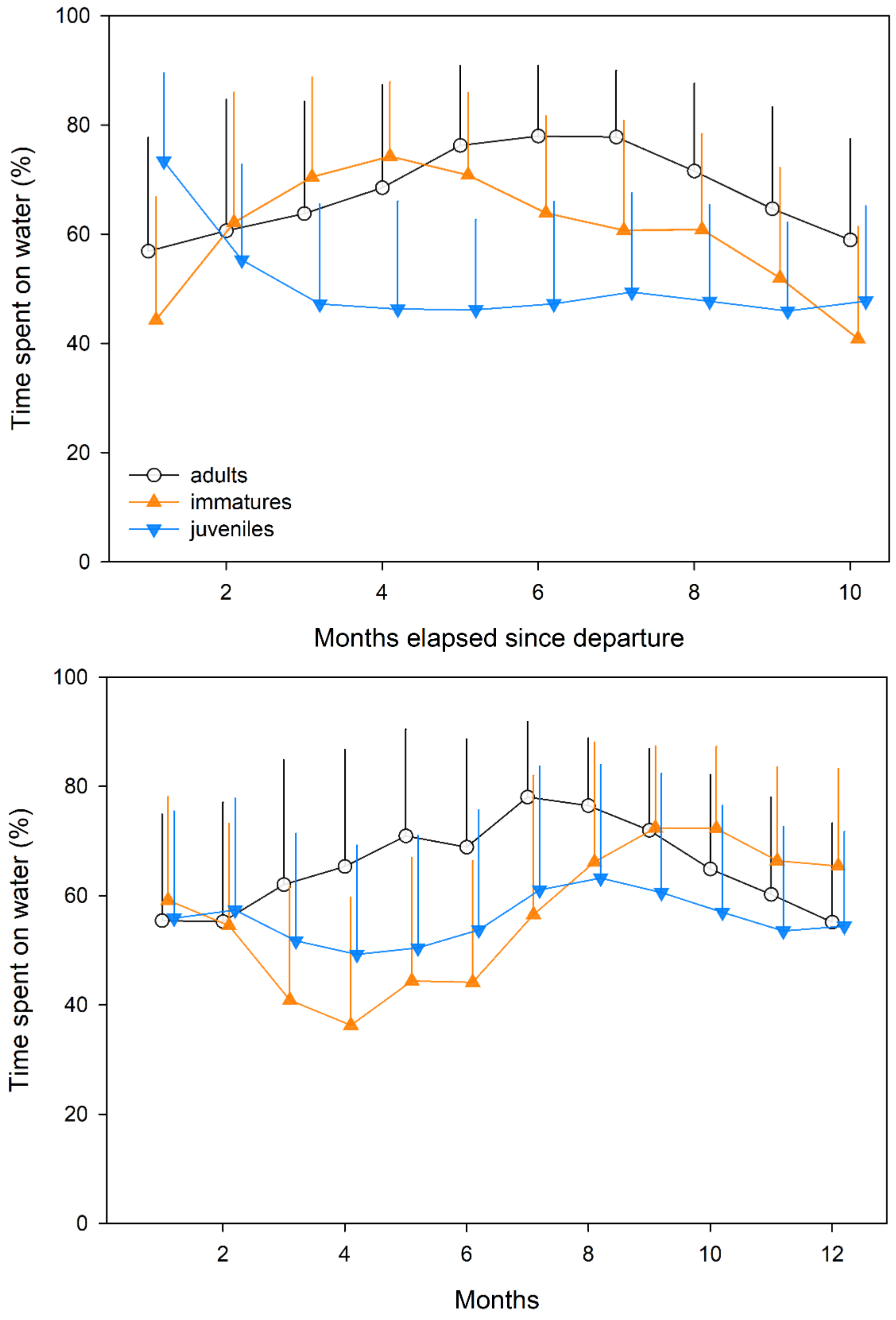


Figure S1 Daily proportions of time spent on water depending on stage (juveniles, immatures and adults) for every month since departure from the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

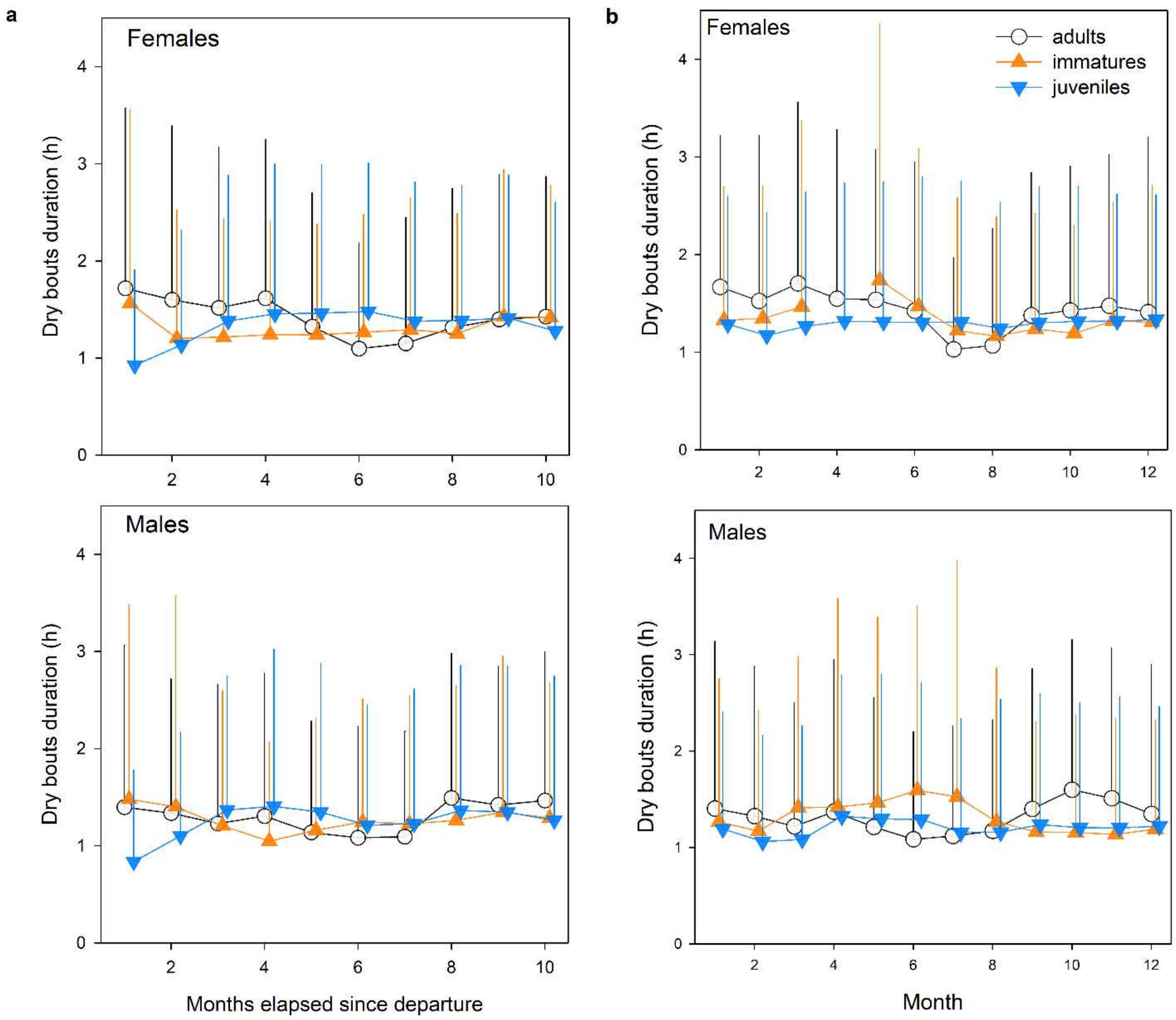


Figure S2 Daily flying bouts duration (dry bouts in hours) depending and on sex (females and males) and on stage (juveniles, immatures and adults) for a) time elapsed since departure from the colony expressed in month (left panel) and for b) each month of the year (right panel). One side error bars represent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

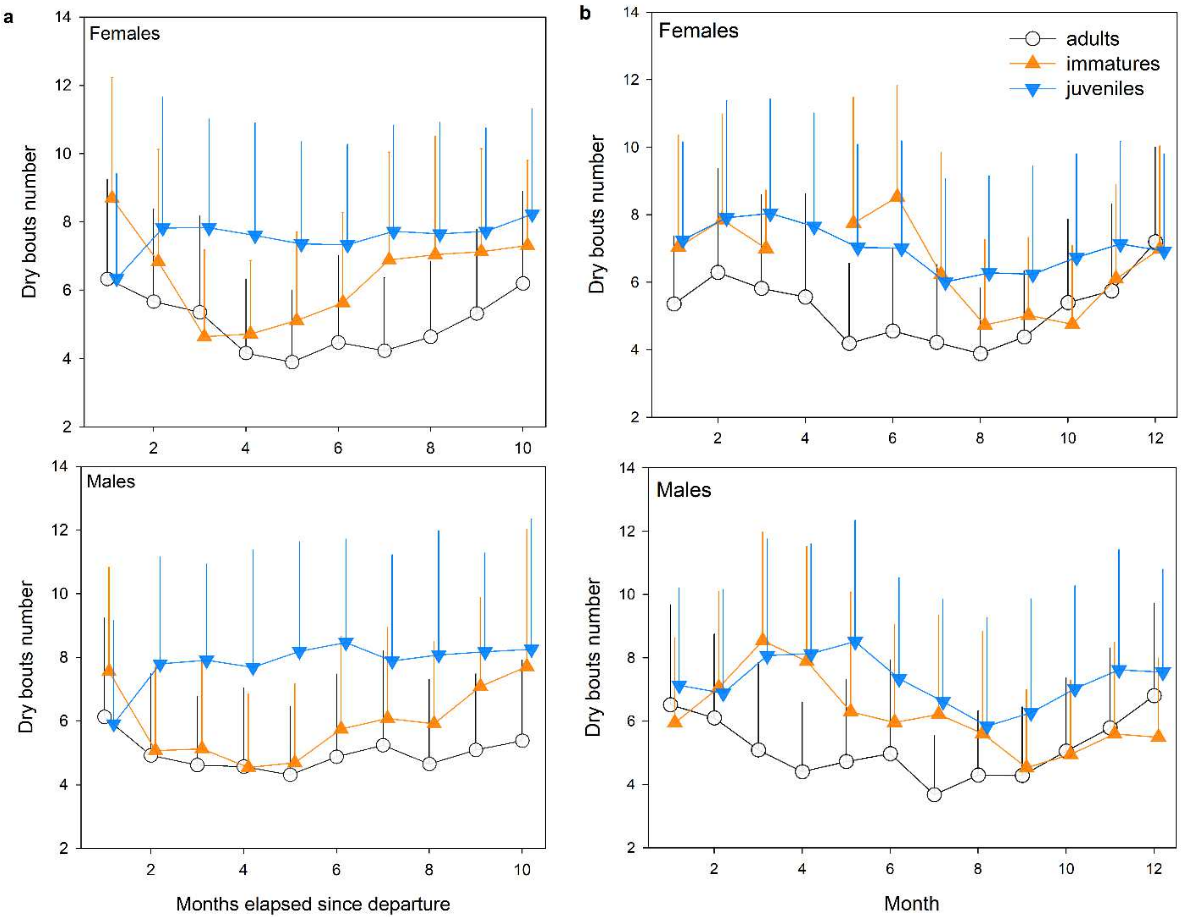


Figure S3 Daily flying bouts number (dry bouts) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

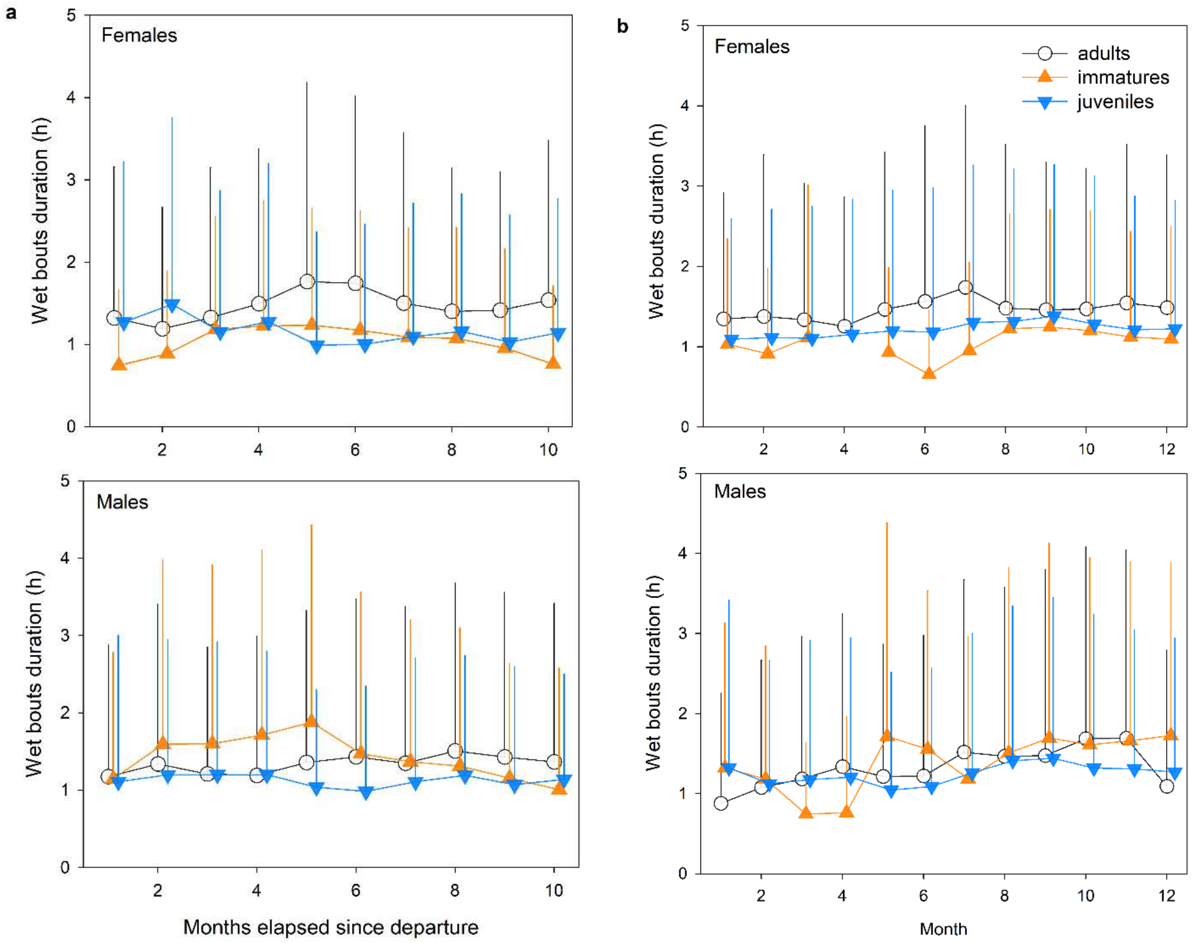


Figure S4 Daily wet bouts duration (bouts on water in hours) depending on stage (juveniles, immatures and adults) and on sex (females and males) for every month since departure of the colony (upper panel) and for each month of the year (lower panel). Error bars represent ± 1 sd

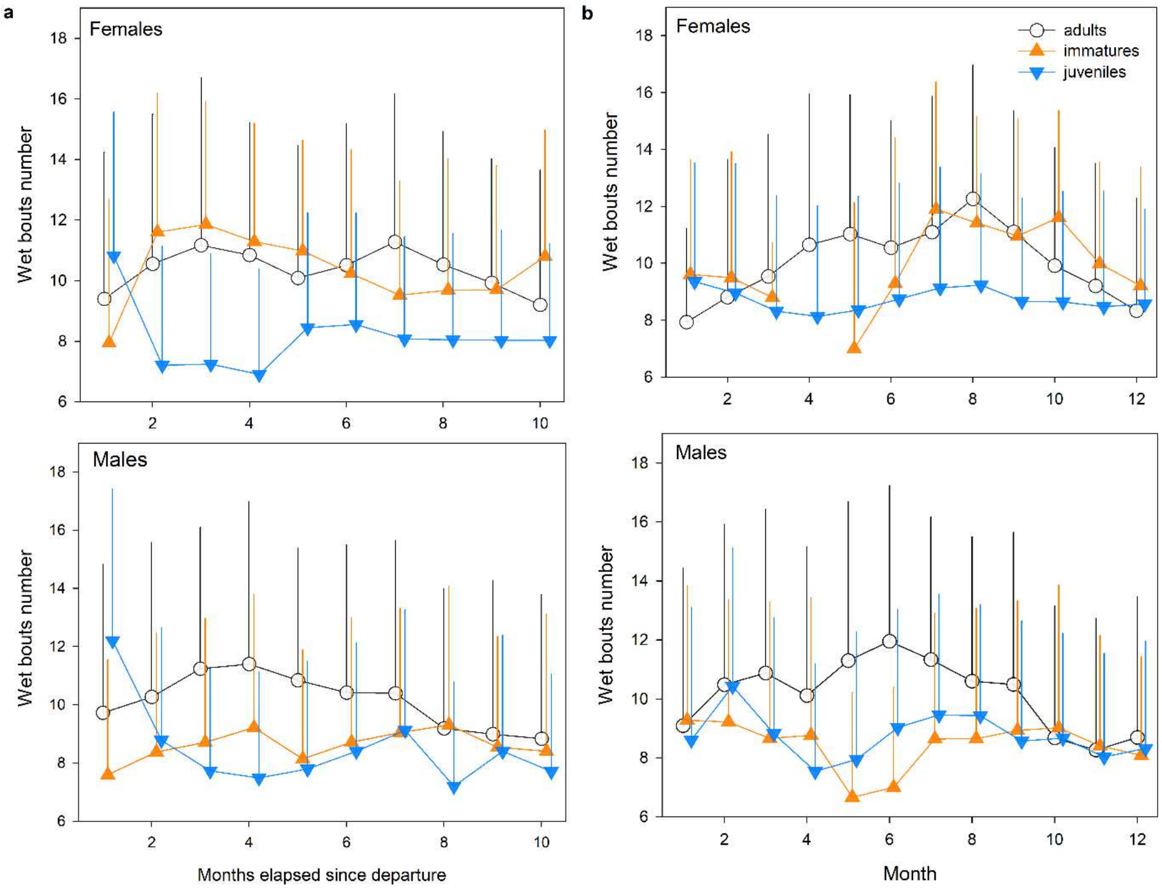


Figure S5 Daily wet bouts number (bouts on water) for every month since departure from the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

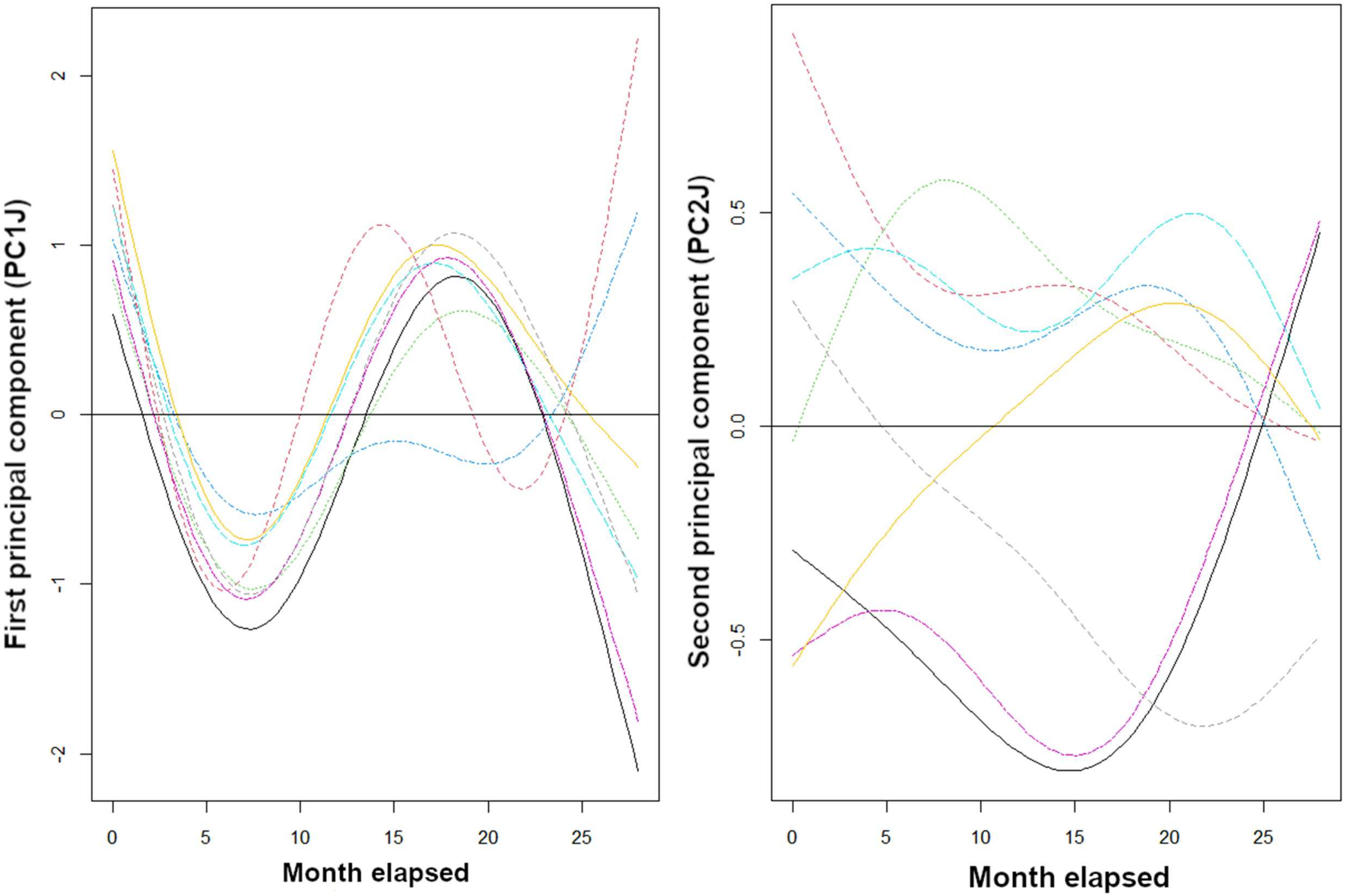


Figure S6 Modeled first (left panel) and second (right panel) axis of principal components analysis of activity parameters of juveniles of Amsterdam albatrosses according to time elapsed (e.g. duration elapsed since departure from the colony expressed in month). Models outputs obtained using random intercepts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

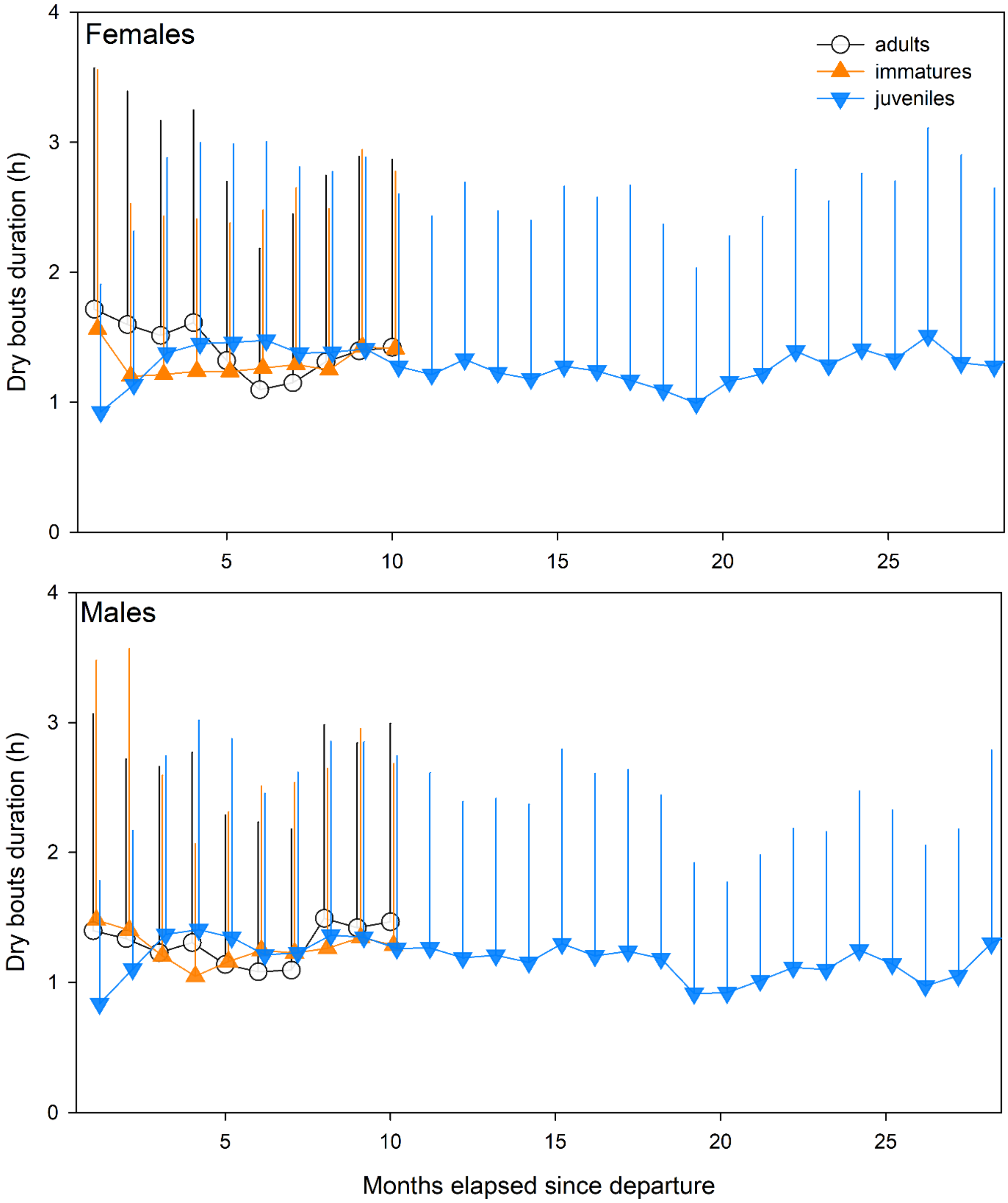


Figure S7 Daily flying bouts duration (dry bouts in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

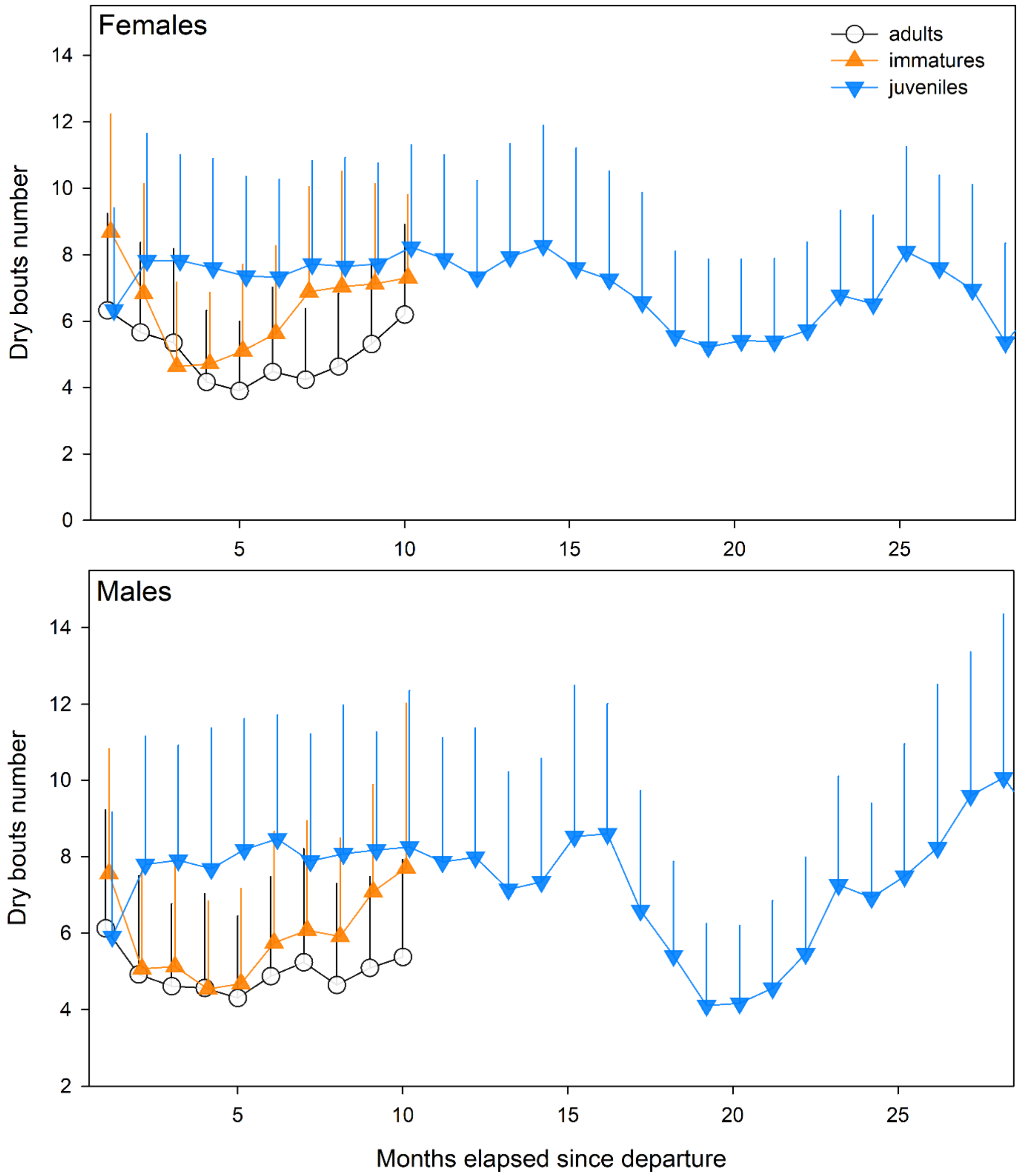


Figure S8 Daily flying bouts number (dry bouts) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

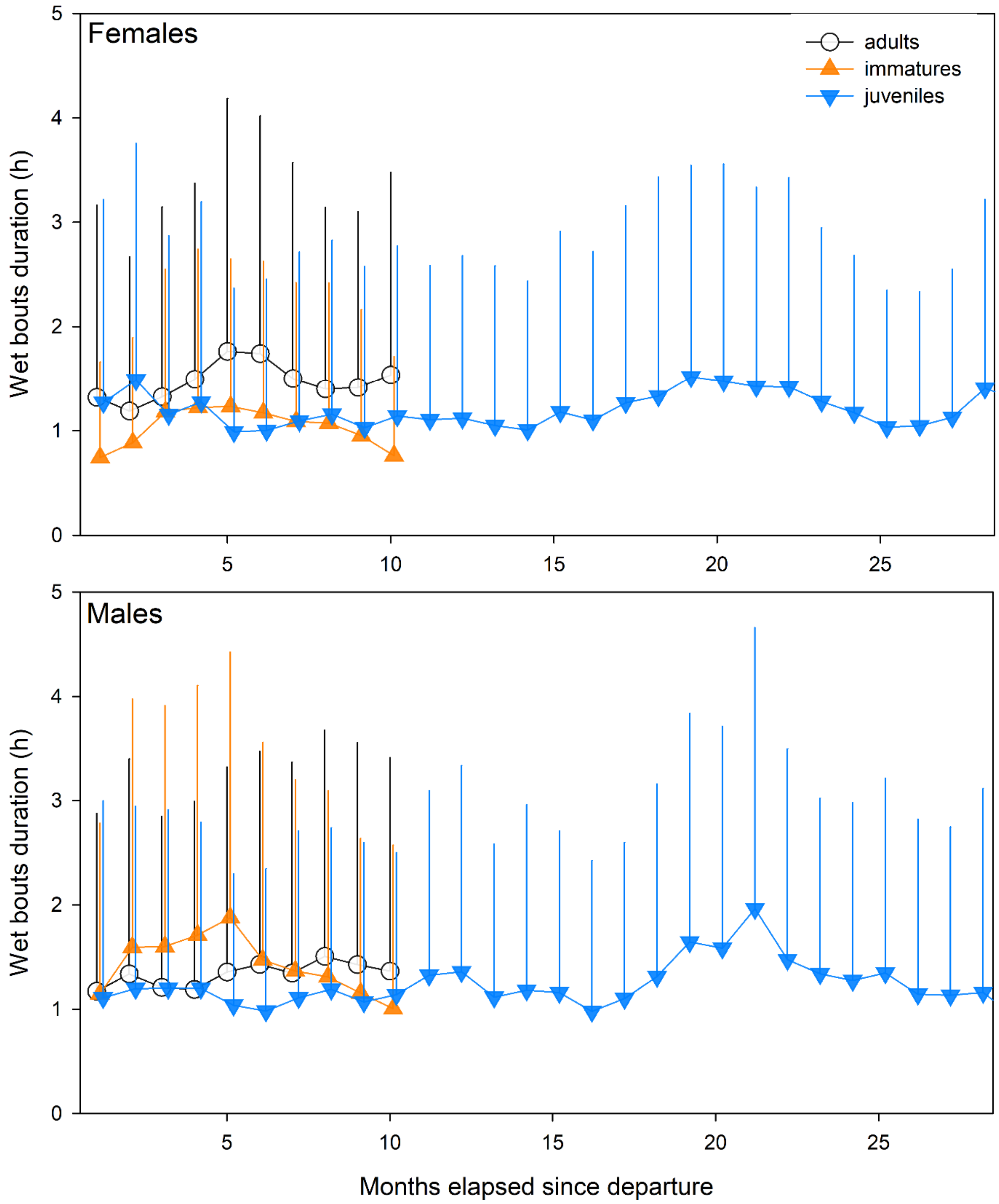


Figure S9 Daily wet bouts duration (bouts on water in hours) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd

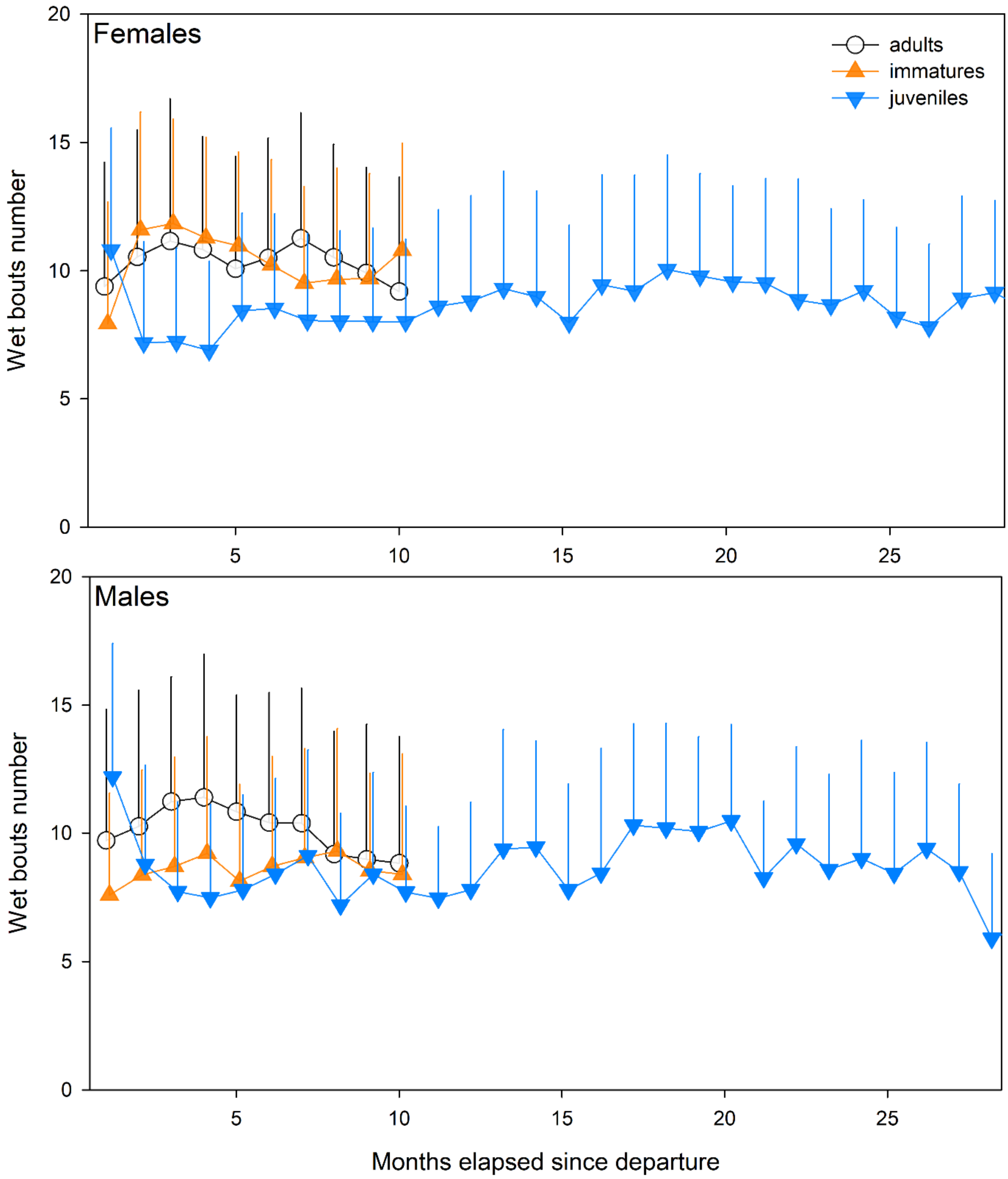
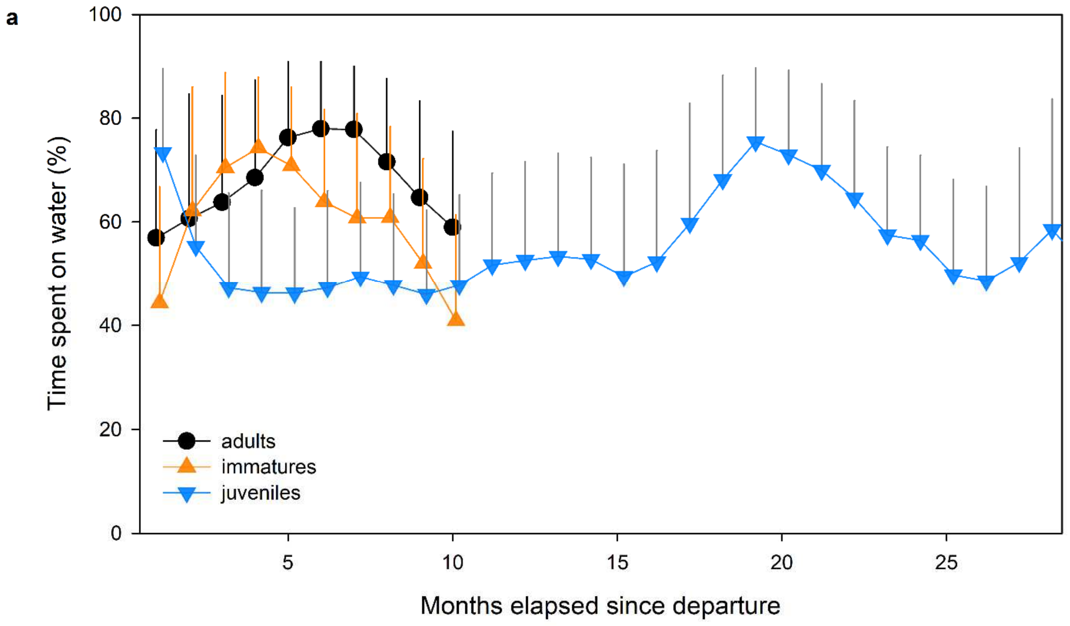


Figure S10 Daily wet bouts number (bouts on water) for every month since departure of the colony for juveniles, immatures and adults for females (upper panel) and males (lower panel). Error bars represent ± 1 sd



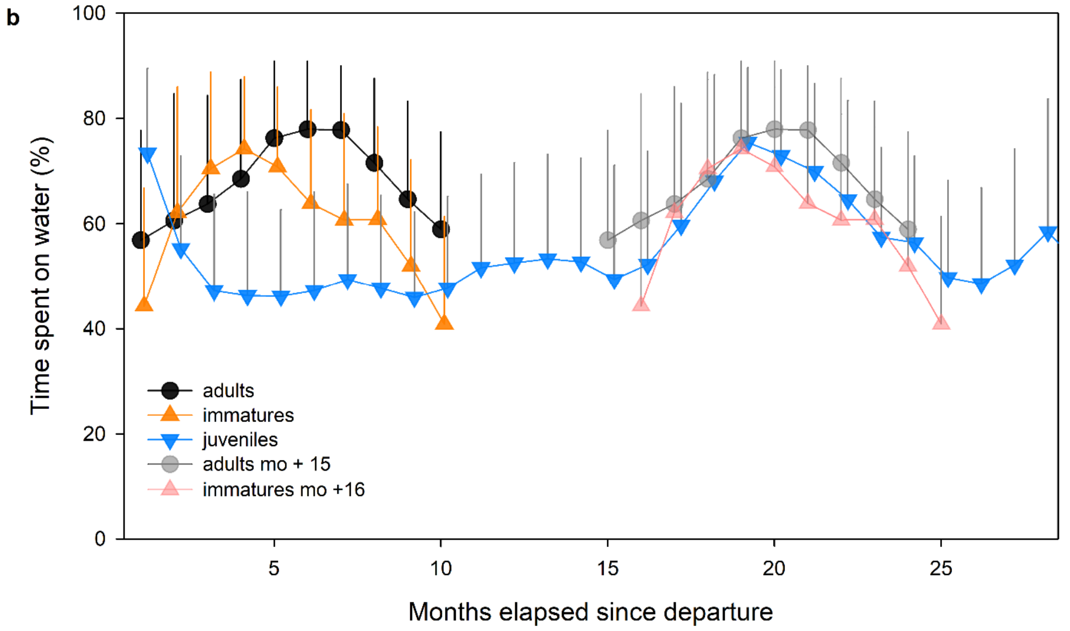


Figure S11 Daily proportions of time spent on water for every month since departure of the colony for juveniles-during the first 28 months spent at sea (after departure), immatures and adults (upper panel) and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel).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

## REFERENCES

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

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

Barbraud C, Delord K, Kato A, et al (2019) Sexual segregation in a highly pagophilic and sexually dimorphic marine predator. bioRxiv 472431

Becker J (2014) Dispersal and Genetic Variation in a Naturally Fragmented Environment: Insights from a Long-term Study of White-throated Dippers (Cinclus cinclus)

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

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

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

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

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

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

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

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

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

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

Corbeau A, Prudor A, Kato A, Weimerskirch H (2020a) Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. Journal of Animal Ecology 89:20–28

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

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

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

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

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

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

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

Evans DR (2018) The post-fledging survival and movements of juvenile Barn Swallows (Hirundo rustica): an automated telemetry approach

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

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

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

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

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

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

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

Harel R, Horvitz N, Nathan R (2016a) Adult vultures outperform juveniles in challenging thermal soaring conditions. Scientific reports 6:27865

Harel R, Horvitz N, Nathan R (2016b) Adult vultures outperform juveniles in challenging thermal soaring conditions. Scientific reports 6:27865

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

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

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

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

Krüger S, Reid T, Amar A (2014) Differential range use between age classes of southern African Bearded Vultures Gypaetus barbatus. PLoS One 9:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Team RC (2019) R: A Language and Environment for Statistical Computing (Version 3.5. 2, R Foundation for Statistical Computing, Vienna, Austria, 2018). There is no corresponding record for this reference[Google Scholar]

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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):

1) **Data, script and code availability (if applicable)**

- **Data, statistical scripts, command lines and simulation code must be made available to readers**. They should either be included in the article or deposited **in** an open repository such as Zenodo **with a DOI**. A perennial URL can be provided if no DOI is available; please note that GitHub URL are not perennial.
- **If deposited in** an open repository, a reference to **Data, statistical scripts, command lines and simulation code**, with a DOI or a perennial URL, must be provided in the reference list and in the "Data, script and code availability" section
- 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**.

When your revised article is ready, please:

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

2) Follow this link https://ecology.peercommunityin.org/user/my_articles or logging onto the PCIEcology website and go to 'For Contributors -> Your submitted preprints' in the top menu and **click on the blue 'VIEW/EDIT' button at the right end of the line** referring to the preprint in question.

3) Click on the black 'EDIT YOUR ARTICLE DATA' button (mandatory step). You can then edit the title, authors, DOI, abstract, keywords, disciplines, and DOI/URL of data, scripts and code. Do not forget to save your modifications by clicking on the green button.

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

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

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

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

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**

---

*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