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TITLE

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

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Abstract

The transition to independent foraging represents an important developmental stage in the life cycle of most vertebrate animals. Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals. Several hypotheses have been proposed to explain higher mortality including that of inadequate/inferior foraging skills compared to adults, young naive 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 successive life stages of the endangered Amsterdam albatross by using miniaturized activity loggers on naive juveniles, immatures and adults. Juvenile naïve birds during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, higher duration and more numerous bouts on water, and lower duration and less numerous flying bouts). Juveniles reached similar activity values to those of immatures and adults as early as the 2nd-3rd months since independence, suggesting a progressive improvement of foraging performances during the first two months since fledging. We found support for the body-size hypothesis with respect to sex differences in activity parameters according to time elapsed since departure from the colony and month of the year, consistent with the important sexual dimorphism in the Amsterdam albatross. Whatever the life stage considered, activity parameters exhibited temporal variability reflecting the modulation of foraging behaviour possibly 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.

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

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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). Juveniles differ from adults in various life history traits and tend to survive less well than adults in most long-lived animals (Ydenberg 1989; Menu et al. 2005; Oppel et al. 2015; Cheng et al. 2019). Several hypotheses have been proposed to explain higher mortality observed for young individuals compared to adults (Healy et al. 2019). One of the most widely accepted hypotheses is inadequate/inferior foraging skills compared to adults, young naive individuals combining lack of experience and physical immaturity (Lack 1954; Daunt et al. 2007). Thus, a change in behaviour, resulting in an improvement of skills acquired from increasing experience is expected to occur during a period of learning through the immaturity phase. 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 especially 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

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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 dispersal juveniles disperse 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 movement patterns of juveniles and adults, namely trajectories (i.e. departure direction or orientation toward specific areas). 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 potentially 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 compare the foraging behaviour, through activity patterns, of naive 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 to infer foraging behaviour (activity) throughout the successive life stages we addressed the following questions: i) do individuals belonging to different life-stages behaved differently? ii) are there

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

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 sex, stage, time elapsed since departure from the colony and seasons which are summarised in Table S1. Given the overlap of spatial distribution between life-stages (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 longer and more numerous bouts in flight; Hypothesis (B), Table 2). We also predict sharp changes in activity following fledging of juveniles from the colony followed by more progressive changes. Based on results found on fledglings wandering albatross (Riotte-Lambert and Weimerskirch 2013; Pajot et al. 2021) showing that juveniles reached some adult foraging capacities in less than two months, we predicted that important changes should be detected in activity parameters early after the juvenile left the colony (within few first months). Overall, juveniles should show higher foraging effort compared to other life-stages (i.e. lower time spent on water, longer flying bouts and shorter water bouts). 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 predict that adjustments of activity will occur according to the time spent (i.e. in months elapsed) since the departure of individuals from the colony (Hypothesis (C), Table 2). In juveniles, we predict early and rapid changes after fledging and then more progressive changes. Due to environmental changes occurring throughout the seasons we predict temporal (i.e. related to the month of the year) changes in activity parameters for all life-stages (Hypothesis (D), Table 2). Although food availability may be lower during winter, foraging effort may also be reduced when adults and immatures are moulting (Weimerskirch

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

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. In this oceanic area, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder sub-Antarctic waters (Belkin & Gordon 1996). 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). However, early failed breeders may start to breed the following year. 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. 1997). 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®

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

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 dispersal 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 dispersal 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 disperse 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 Procellariiforme species.

Global Location Sensing (GLS) loggers were 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). Immersion loggers tested for saltwater immersion every 30 s, storing the number of samples wet (>0) at the end of each 10 min period. We used

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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 nonbreeding 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 2). 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 proportion of time in seawater at 10 min intervals, which we summarized as hours in the water per day (PROWATER; 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 WETBOUTS). 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 DRYBOUTS). Additionally the numbers of bouts (bouts on water: WETBOUTSNB and bouts flying: DRYBOUTSNB) were obtained daily. Although the

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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 (WETBOUTS) > 1h based on PTT tracking data (Weimerskirch et al. unpublished data); 2) immatures and adults, the last bout spent flying (DRYBOUTS) > 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

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

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

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

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

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

Models for PROPWATER, WETBOUTSNB and DRYBOUTSNB including all combinations of explanatory variables 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.

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

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

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

Results

Male Amsterdam albatrosses were larger than females, particularly for tarsus length and bill length and bill depth whatever the stage (juvenile or adult; see Supplementary A Table S2-S7). In juveniles, males were ~13% heavier than females, while the difference was not significant in adults. 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.

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

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

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

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

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

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

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

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

Discussion

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). By comparing changes in behaviour at sea and foraging parameters of juveniles up to 28 months 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 patterns. During the first month following their departure from the colony juveniles spent a greater proportion of time sitting on water, did longer and more numerous bouts on water, and shorter and less numerous flying bouts than immatures and adults. However, from the second month following departure from the colony this pattern reversed and the activity patterns of juveniles became similar to that of immatures and adults only 10 to 17 months after fledging depending on the activity parameter considered (see Figure 6). Together, these results suggest a progressive improvement of movement performances during the first two months since fledging. Juvenile naïve birds during their first month at sea after leaving their colony exhibited lower foraging effort (greater proportion of time spent sitting on water, higher duration and more numerous bouts on water, and lower duration and less numerous flying bouts). They reach values similar to those of immatures and adults 2 to

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3 months after departure (except for the number of dry/wet bouts for which it took longer), suggesting a progressive improvement of foraging performances during the first two months since fledging. This suggests that juvenile individuals are therefore very likely to have poorer foraging skills during their first two months spent at sea. Since all stages of the Amsterdam albatross forage in the same water masses (see Thiebot et al. 2014), differences in foraging behaviour were not due to different oceanographic characteristics as observed in other species (Thiers et al. 2014; Weimerskirch et al. 2014; Frankish et al. 2020b). These lower performances 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). It is likely that increasing exposure to diverse foraging situations allows juveniles to rapidly accumulate foraging experience and improve various aspects of foraging.

The lower performance of juveniles we found 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, which found that shortly after fledging juvenile albatrosses employ similar foraging strategies as adults. Additional 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). 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 flew large distances from the colony (Frankish et al. 2020).

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

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

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. We found support for the body-size hypothesis to explain sex differences in activity parameters (except for the time spent on water), consistent with the important sexual dimorphism in the Amsterdam albatross. Males tended to spend more time sitting on water (wet bouts duration) whatever the stage, and depending on stage more (for juveniles) or less (for immatures and adults) frequently compared to females. Consistently, we found that males tended to fly for shorter periods (dry bouts duration) compared to what females did and possibly less frequently (dry bouts number) depending on time. Whatever the stage, there was no significant effect of sex on the proportion of time spent on the water (except in immatures where males tended to spent more time sitting on water compared to females).

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). Although Amsterdam albatross is 5-8% smaller and 25% lighter than wandering albatross, the two species have a very close anatomy and similar use of the wind. In the wandering albatross, due to sex differences in flight performance, specifically, due to their higher wing loading, males should both maintain longer flying effort and be more likely to minimize the number of flying bouts than females (Shaffer et al. 2001; Clay et al. 2020). Hence, 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

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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*'). In other word, males may have more of a '*sit-and-wait*' strategy while females have more of a '*foraging-in-flight*' strategy, although there is some behavioural plasticity particularly over time. Our prediction that foraging behaviour differs between sexes was fully supported (i.e. sex-differences in bouts duration and number). Nevertheless, the similarity in time spent on the water suggests that the differences may be more subtle, showing some a trade-offs in duration and numbers between flying and water bouts. This trade-off should vary depending on stage as immature females tended to have shorter and more frequent bouts on the water. This implies that while probably feeding on similar water masses, the sexes might differ in type of prey targeted and/or used different foraging methods. The confirmation of this hypothesis reinforces the fact that the two-sibling species, as previously assumed, show a high degree of similarity in their foraging behaviour.

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. 2019). 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), 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 females Amsterdam albatross have a greater advantage in foraging in the subtropical environment than

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

Both extrinsic (i.e. environmental conditions: variability in subtropical waters resources or in wind) 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 of activity parameters we found whatever the stage. Subtropical environments in the southern Indian Ocean are generally characterized as oligotrophic areas but nonetheless are known to vary over the seasons. During the austral winter, colder surface waters and strong winds result in changes of oceanographic conditions associated with an increased primary productivity (Behera and Yamagata 2001; Terray 2011; Delord et al. 2021). Changes in water temperature associated with wind appear to result in seasonal biological production variations, however, the delay between the increase in primary production and the increase in potential prey for albatrosses is probably rather long in this oligotrophic context. These changes were found to affect seabirds (Delord et al. 2021). Part of the activity changes observed following the departure of juveniles Amsterdam albatross could reflect 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 albatrosses.

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

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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. 2015, 2020). Interestingly, immature appear to have this peak in time spent on the water in spring, suggesting different timing of moult.

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

Stage[1]	Definition	Age[1]	Tracking duration	Behaviour
Juvenile	Following chick fledging in January	1st year	~2.5 years	Chicks disperse at sea after leaving the colony for the first time
Immature	After juvenile dispersal, until first breeding attempt (at 9 year old on average)	~2-10 years	~1 year	Nonbreeding young birds forage at sea and occasionally visit the colony for mating
Adult sabbatical	Between two successive breeding periods (~ 15 January year *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

440 [1] Stage/Age at which the individuals were equipped with loggers in our study

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

Stage	Years of deployment	Deployed (n)	Recovered (n)	Recovery rate (%)	GLS with data (n)
Juvenile	2011	21	12	57 (*t*+9)	10
Immature	2011-2012	18	17	94	13
Adult sabbatical	2006, 2009	11	11	100	10

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

444 albatross

445

	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

446 [1] calculated during 28 months following departure; [2] calculated during 9 months following departure

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FIGURES

Figure 1 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 2 Daily flying bouts duration (dry bouts in hours) depending on stage (juveniles, immatures and adults) and on sex (females and males) 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 3 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 ± 1s.d.

Figure 4 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 5 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 6 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)

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and with a 15-16 months of delay for immatures and adults compared to juveniles (lower panel). Error bars represent $\pm$ 1 sd.

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Figure 1

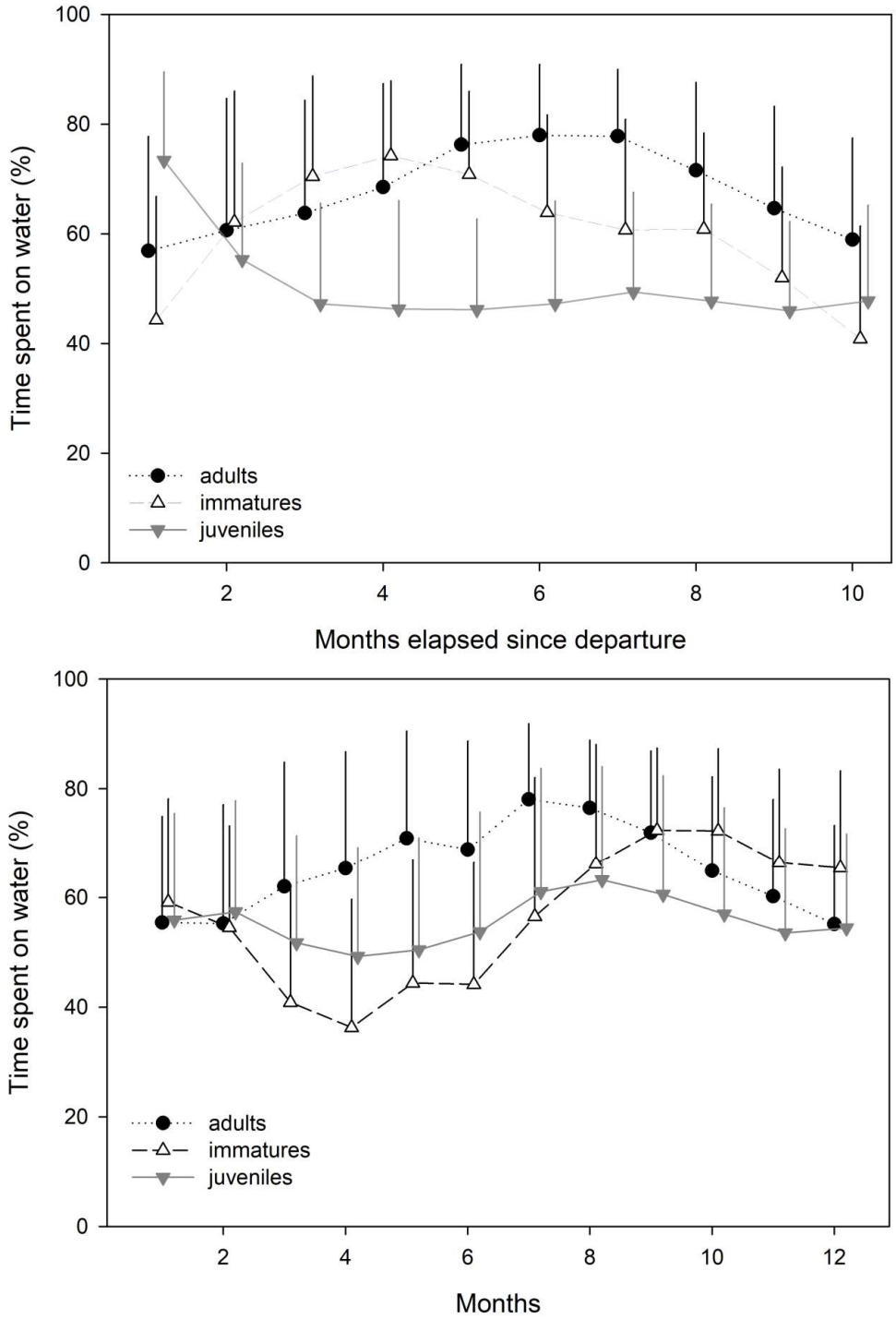

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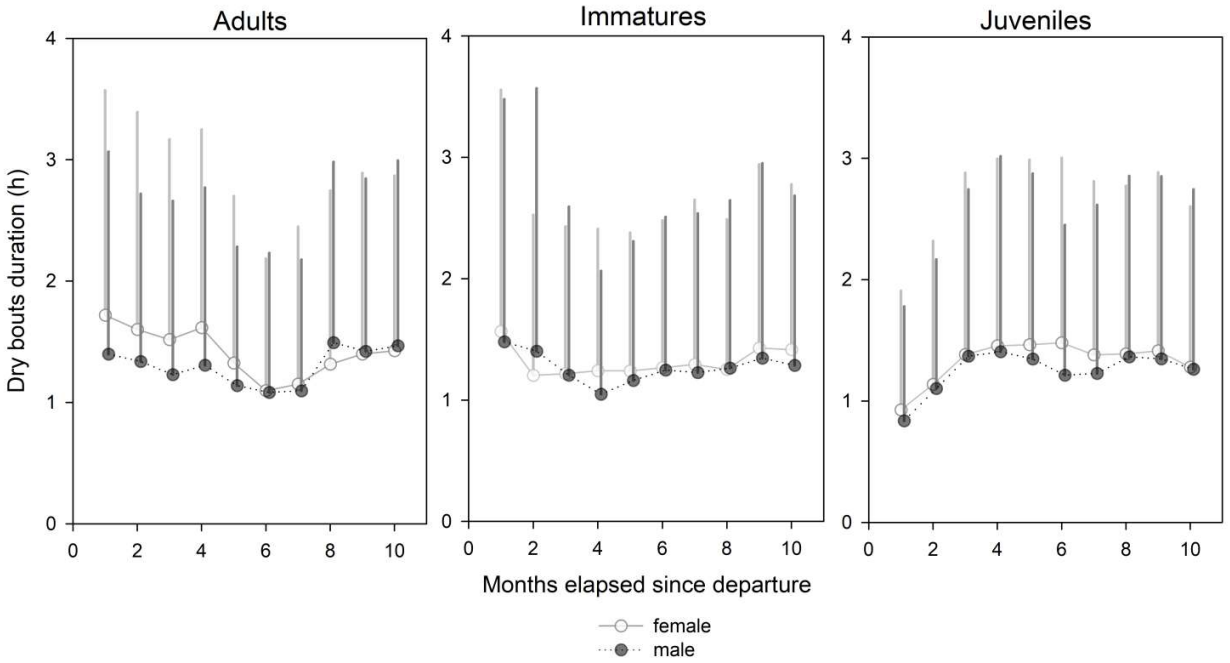
Figure 2



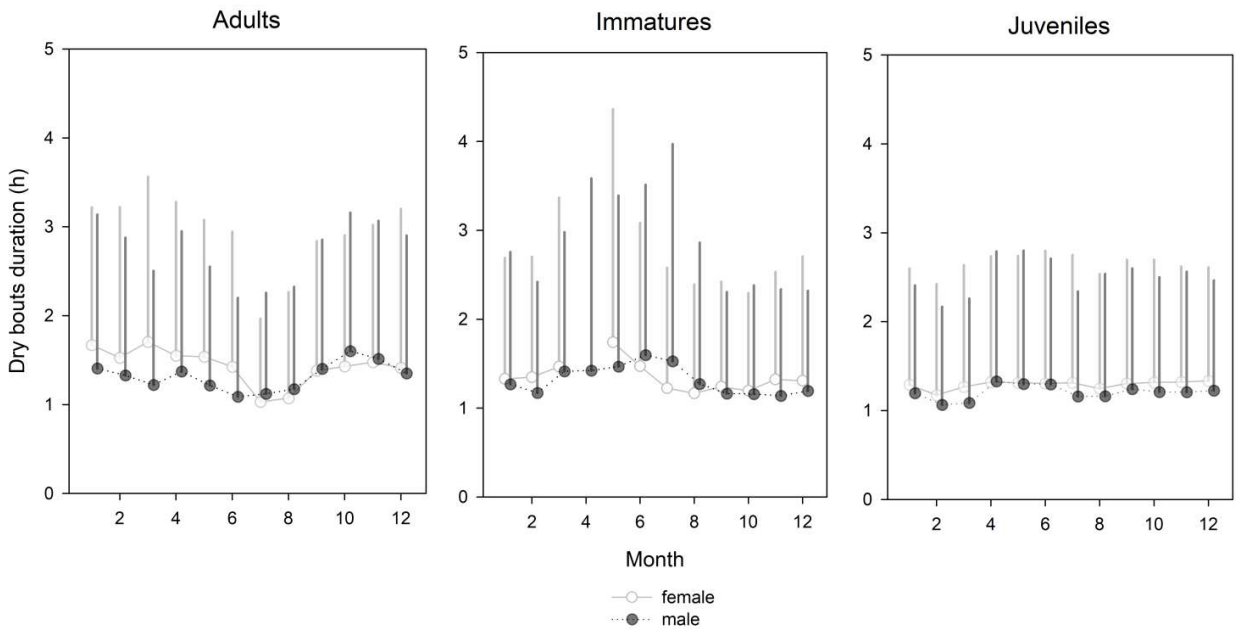


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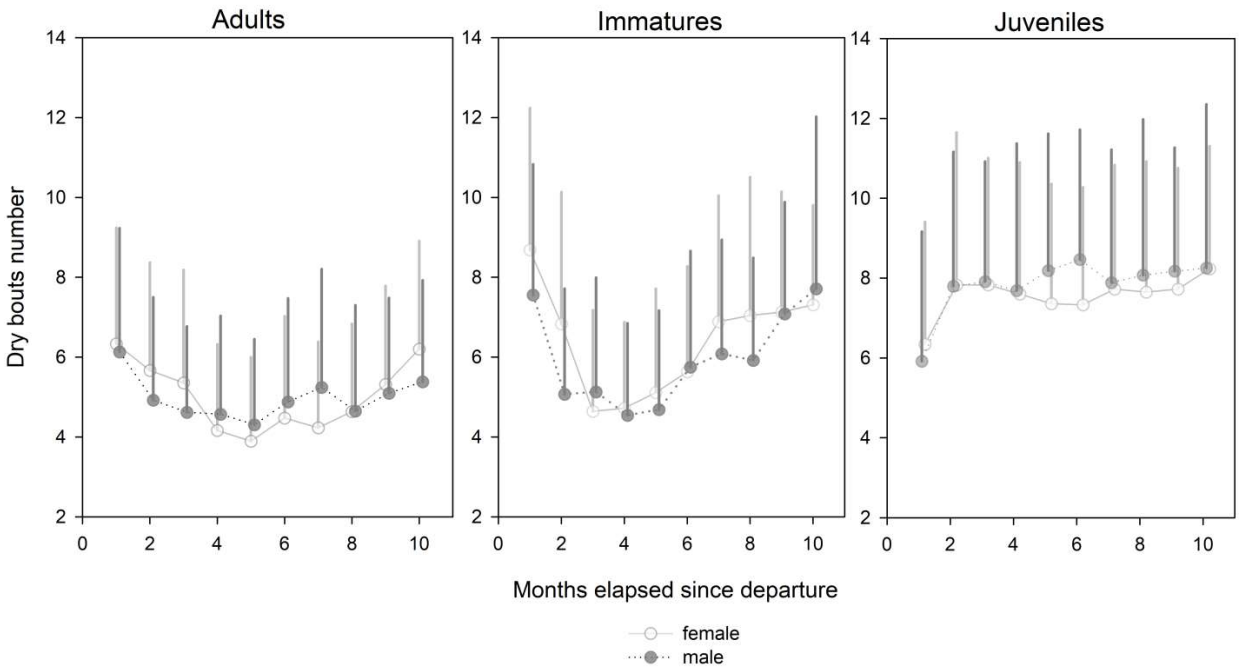
Figure 3



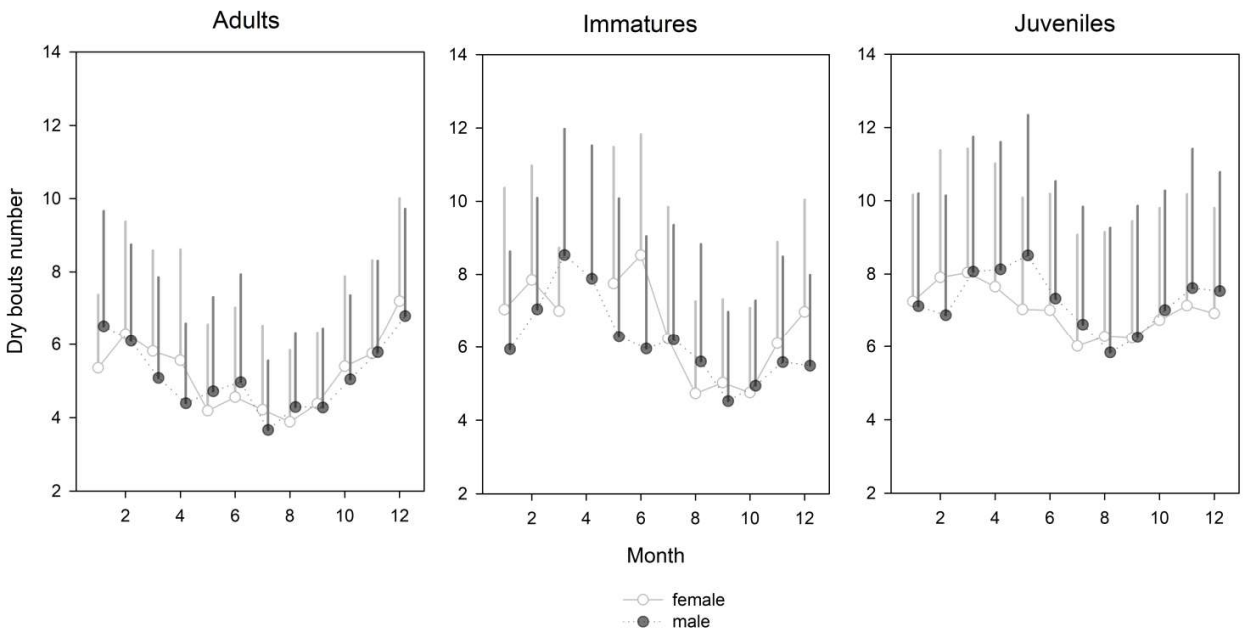


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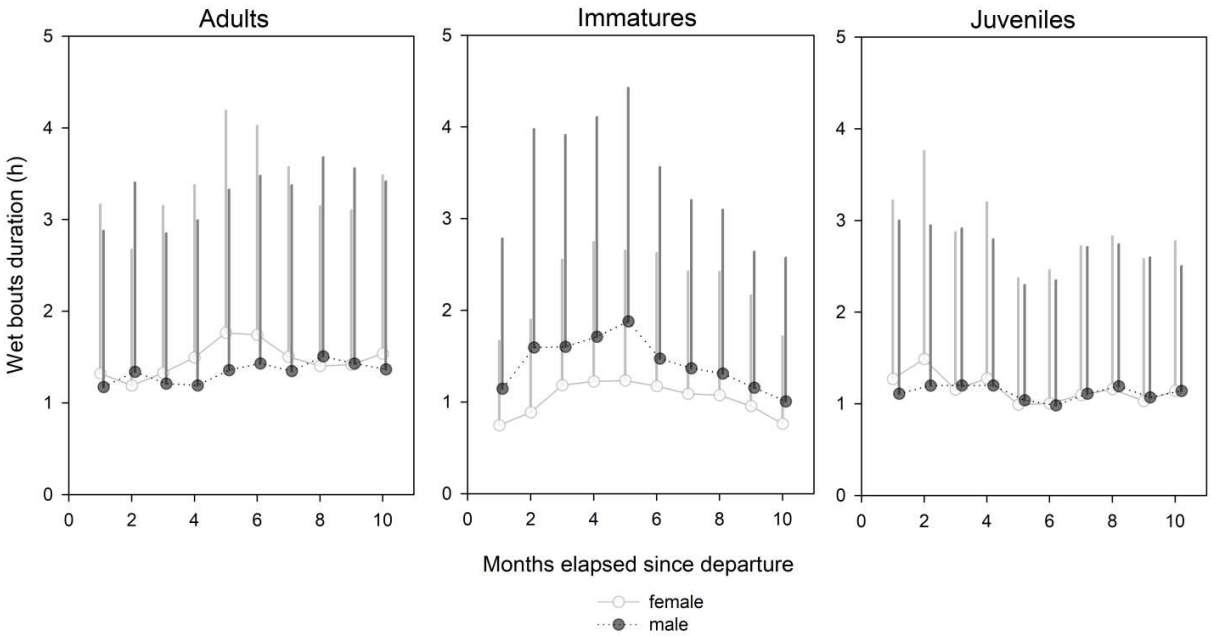
Figure 4



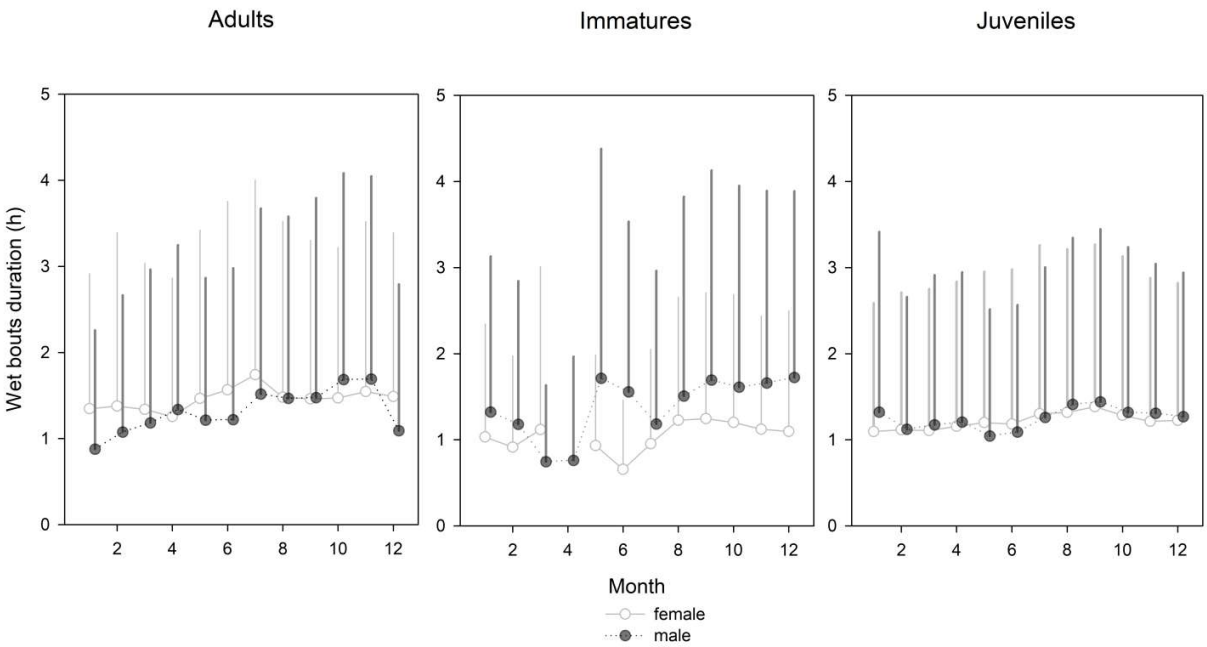


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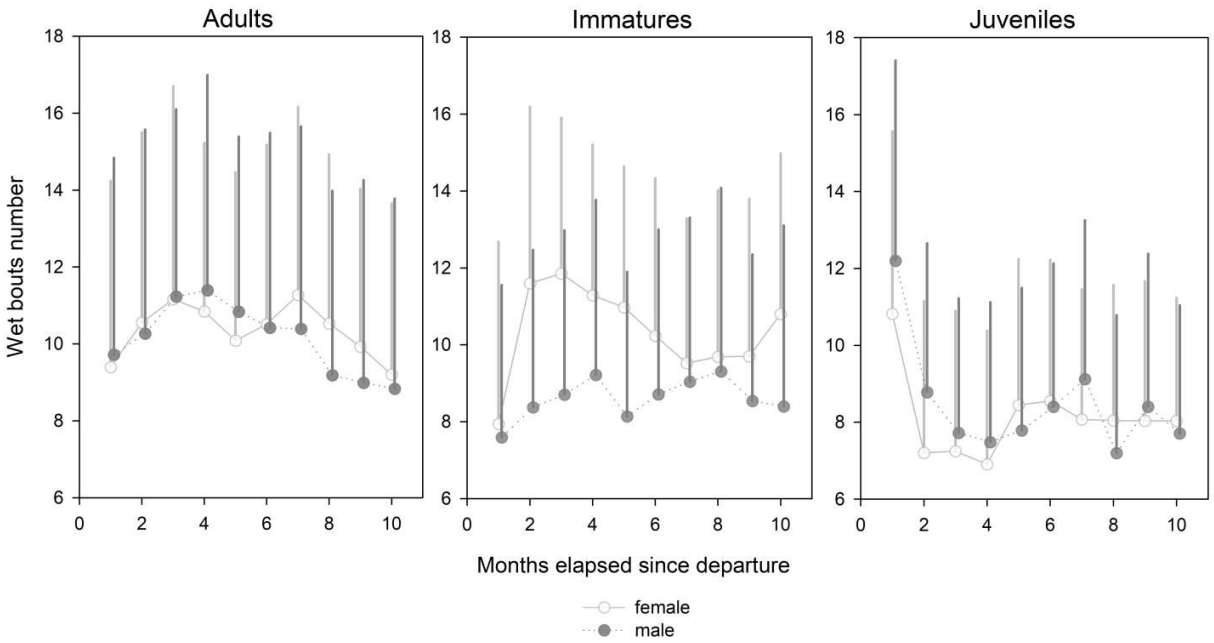
Figure 5



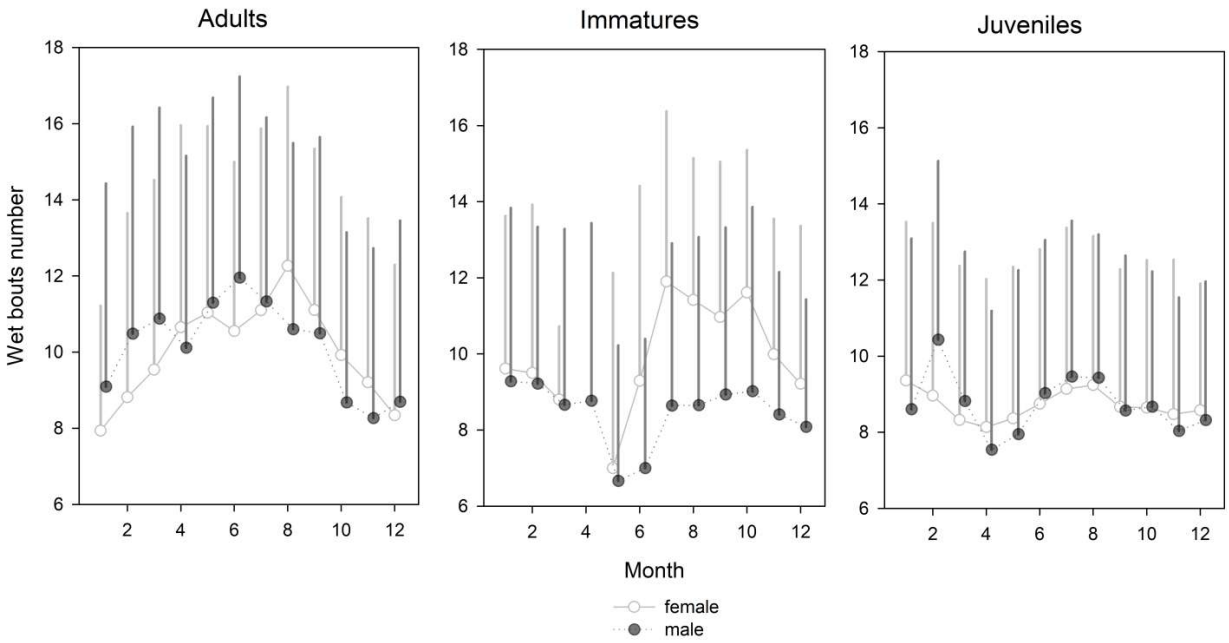


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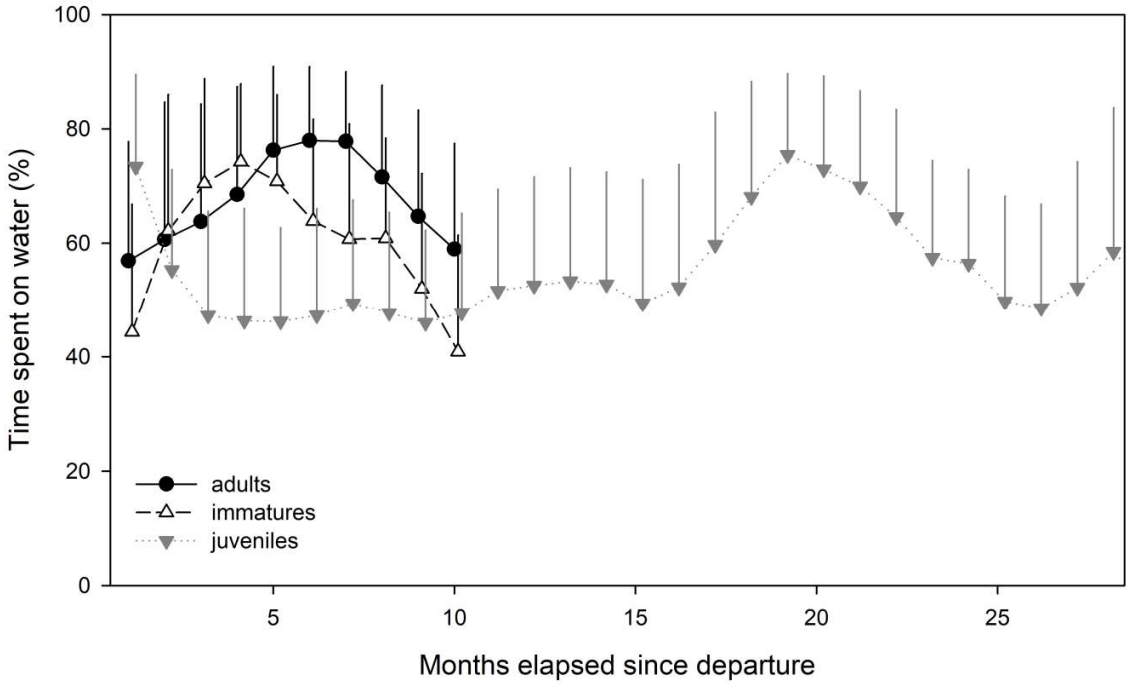
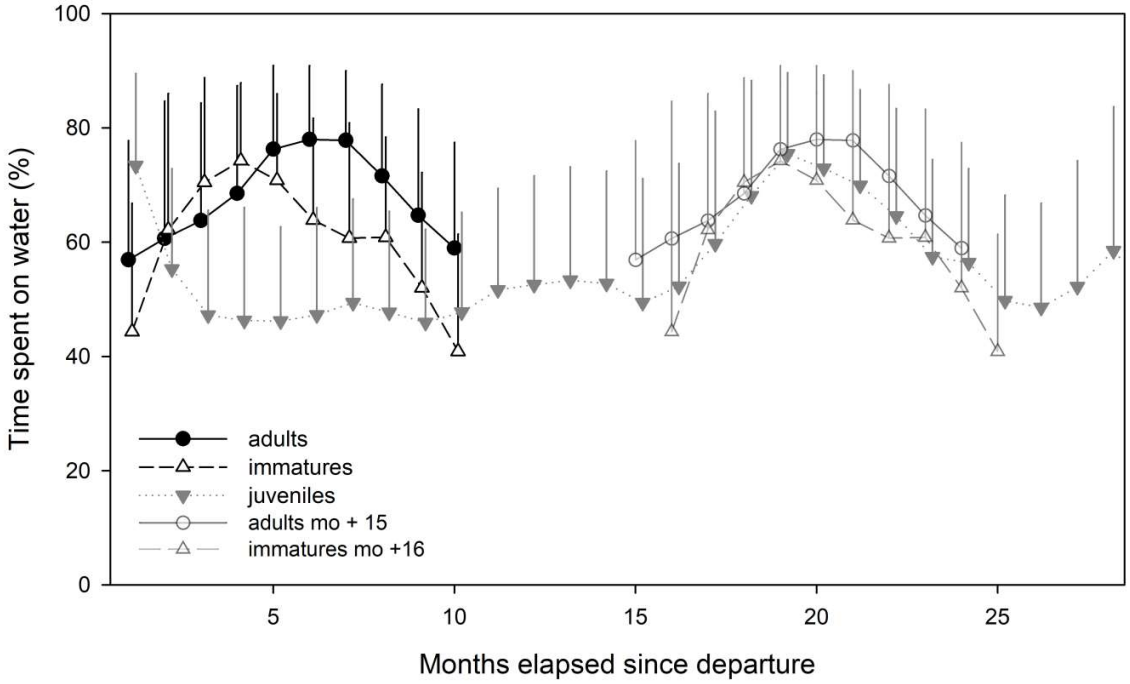
Figure 6





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