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Article

Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour

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The first year of life is a period of high mortality in animals. Reduced foraging capacities of naive individuals might be the primary cause of their mortality. These capacities are supposed to be progressively acquired during the first months of life. In this study, we investigate the ontogeny of flight capacities, by day and night, of first-year individuals, and compare it with adults from two closely related species of great albatrosses: Amsterdam *Diomedea amsterdamensis* and wandering *Diomedea exulans* albatrosses which forage in different environmental conditions. We used 71 tracks of 71 juvenile birds and 141 of 116 incubating adults to compare both age categories. In order to explore the effect of moon light on night activity, we elaborated a new formula which improves the precision of the proxy of moon illumination. By day, we found that juveniles of both species reach some adult foraging capacities in less than two months. By night, albatrosses have reduced activity increasing during the first weeks at sea for juveniles and changing in accordance with moon illumination for both juveniles and adults. A peak of flight activity at dawn and dusk was apparent for both species. Interspecific comparison underlined that Amsterdam albatrosses were more active than wandering albatrosses, suggesting a difference in food and foraging strategy. Overall, we highlighted how life history traits, environmental conditions and time of the day affect the foraging activity of two related species of seabirds.

Keywords: albatross, diel activity pattern, *Diomedea*, flight behavior, foraging activity, moon illumination, night activity, seabirds

Introduction

In seabirds, as in many other animal species, survival of juveniles during their first year at sea is low. Drivers of this mortality are not fully understood. One of the most recognized and studied hypothesis considers that first-year animals are physically immature and lack experience, resulting in inferior foraging and movement abilities (Lack 1954, Ashmole 1963, Lindström 1999). Therefore, it is assumed that juveniles acquire abilities during their early-life, reaching an optimum behavior by themselves or with experienced individuals (Clutton-Brock et al. 2001, Mazur and Seher 2008, Rotics et al. 2016).



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Learning of foraging techniques during early-life has been previously studied in different species (e.g. primates (Lefebvre 1995), bears (Mazur and Seher 2008), dolphins (Fragaszy and Perry 2008), seals (Breed et al. 2011) or insects (Boivin et al. 2010)). For seabirds in particular, where juveniles leave the colony alone, there is an increasing number of studies focusing on the first year of life (MacLean 1986, Yoda et al. 2004, Daunt et al. 2007, Péron and Grémillet 2013, Riotte-Lambert and Weimerskirch 2013, Campioni et al. 2019, Ramos et al. 2019, Collet et al. 2020, Corbeau et al. 2020) and the immature period (Péron and Grémillet 2013, Riotte-Lambert and Weimerskirch 2013, Clay et al. 2018, Campioni et al. 2019). However, studying this period of learning at sea is challenging for oceanic species such as albatrosses since they do not return on land before the fourth or fifth year, and cover huge distances in extreme oceanic conditions (De Grissac et al. 2016). With the recent development of new sensors and biollogging technologies, it is now possible to follow birds for a longer time, to have more precise locations and store many data, considering the habitat of the bird (Harcourt et al. 2019, Yoda 2019).

Using these technologies, Yoda et al. (2004) were the first to study daily changes of flight behavior on captive-bred seabirds, investigating parameters such as duration of foraging trips, time spent gliding and proportion of time spent in flight. Subsequent studies (Daunt et al. 2007, Péron and Grémillet 2013, Riotte-Lambert and Weimerskirch 2013, Clay et al. 2018, Ramos et al. 2019, Collet et al. 2020, Corbeau et al. 2020) explored juveniles' behaviors and their changes over time and compared it to adults. All highlighted that some parameters of juveniles' flight behavior improved to attain adults' ones but in variable time durations and assumed that the long immaturity of seabirds was partly due to this long period of learning. Other parameters were considered as innate (Riotte-Lambert and Weimerskirch 2013). These studies indicate that the duration of the acquisition of foraging abilities varied between species (De Grissac et al. 2016). These differences could be related to the fact that they belong to different taxonomic groups and/or forage in very contrasted environments (tropical versus temperate or polar) with different ranges of sea surface temperature, wind, resource availabilities, night duration and light conditions.

Although many seabirds are not active in complete darkness, many species take advantage of illuminated nights to increase foraging effort. This aspect, to our knowledges, has never been studied in juvenile seabirds. In adult seabirds, at-sea night activity varies among species (Harper 1987, Weimerskirch and Guionnet 2002, Phalan et al. 2007, Mackley et al. 2010) from low for wandering albatrosses – *Diomedea exulans* (Weimerskirch and Wilson 1992, Weimerskirch et al. 1997b) to high for white-chinned petrels – *Procellaria aequinoctialis* (Mackley et al. 2011) or even exclusively at night in swallow-tailed gull – *Creagus furcatus* (Cruz et al. 2013). Night-behavior of albatrosses, particularly from great albatrosses of the *Diomedea* genus, is assumed to be reduced probably because they are less able to fly and find prey in darkness (Weimerskirch et al. 1997b, Phalan et al.

2007). Nonetheless, seabirds' at-sea night activity changes with moon illumination (Yamamoto et al. 2008, Pinet et al. 2011, Regular et al. 2011, Cruz et al. 2013), which increases visibility and improves detection of prey. Furthermore many prey such as zooplankton, squid and fishes do a diel migration and approach sea surface at night (Gliwicz 1986b, Luecke and Wurtsbaugh 1993, Hays 2003). This phenomenon is moon-dependent as it decreases in intensity during bright nights (Gliwicz 1986a, Lowry et al. 2007) which possibly impacts foraging strategies of albatrosses mainly feeding on cephalopods and small fishes (Cherel and Klages 1998, Imber 1999, Cherel et al. 2017).

In this paper we studied daily changes in the flight behavior of juveniles of two closely related albatross species, Amsterdam albatross – *Diomedea amsterdamensis* (Roux et al. 1983) and wandering albatross – *Diomedea exulans* (Linnaeus 1758). While wandering albatross has been the subject of many studies on its foraging ecology since the first tracking studies (Jouventin and Weimerskirch 1990), Amsterdam albatross, an endemic species of the Amsterdam island, has only been recently described (Roux et al. 1983) and little is known on its ecology at sea, especially during non-breeding stages (Thiebot et al. 2014). Although closely related, both species live in two different habitats with different constraints: Amsterdam albatross is a subtropical species throughout its life cycle (Thiebot et al. 2014) whereas wandering albatrosses forage over a more varied number of habitats, especially in subantarctic and Antarctic waters.

In this study, we compared the first months at sea of juvenile birds from both species in order to examine differences in the foraging and movement ecology during a critical period for their life. We examined whether juveniles improve their foraging efficiency to attain those of adults for two flight parameters: proportion of time spent flying and speed, during daytime, but also at night, according to light intensity.

We wanted to test several hypotheses:

- 1) Acquirement of foraging skills by juveniles should be gradual and might differ between both species. Acquired skills might be different from adults.
- 2) Light availability at night may affect juveniles differently from adults; because of their lower foraging abilities during the first months, juveniles may spend more time foraging at night to increase foraging time.
- 3) A higher moon illumination should affect night behavior of albatrosses by increasing their flight time. Juveniles might be less affected because of their lower foraging abilities.
- 4) Because each species forages in different environmental conditions, foraging strategies might differ between Amsterdam and wandering albatrosses in both age categories.
- 5) As bycatch rates by long-liners were high during twilight (Murray et al. 1993), flight activity is expected to be more important around dawn and dusk, when diel vertical migration is still undergoing, and visibility higher than at night.

Material and methods

Loggers technology and deployments

Two types of loggers developed by Sextant Technologies (New Zealand), measuring precise GPS locations, were used for this study:

- XArgos satellite transmission loggers (55 g, 109 × 30 × 19 mm), programmed to record and send a location every hour. Deployed on juvenile birds, loggers were attached on the back feathers using Tesa tape (Tesa, Germany) and thus should remain on the bird for several months, and at the latest until the first moult (maximum after nine months).
- Centurion data archival loggers (65 g, 109 × 30 × 22 mm), programmed to record a location every two minutes. Deployed on incubating breeders, loggers were attached to the back feathers only using Tesa tape in order to remove them after one, two or three trips at sea. Each track represents a foraging trip. Data were downloaded after the logger was removed from the bird returning from a trip.

The loggers weigh respectively 55 g and 65 g which represents between 0.4% and 0.7% (median = 0.6%) of the body mass of juveniles for the first, and between 0.5% and 0.9% (median = 0.8%) of the body mass of adults, much less than the 3% recommended (Phillips et al. 2003).

During three consecutive fieldwork campaigns between 2017 and 2019, 103 juvenile albatrosses ready to take off were equipped at Crozet, Kerguelen and Amsterdam Islands, providing 71 tracks (Table 1). As a comparison, we used 141 complete tracks from 123 incubating breeders equipped in 2017 and 2018 on the three islands (Table 1). We used complete foraging trips for adults and trips lasting at least five days (maximum time to reach 100 km from the nest) before the logger stopped transmitting for juveniles or juveniles died. We found no case of transmitters drifting during two days or more before stopping transmitting, which may have resulted from a dead bird floating at the surface.

Details of the loggers and deployments are given in Weimerskirch et al. (2020).

Data processing

In order to perform similar standardized analyses, we resampled the Centurion data to obtain hourly locations for adults. With 187 loggers we collected 244 tracks on which we applied various filters. After having removed spurious

Argos score locations (cyclic redundancy check was generated for each location, we kept CRC = ‘OK’ and removed CRC = ‘Error’), duplicates and all (but the last) location on land before departure, we applied a speed filter (120 km h⁻¹ (Weimerskirch et al. 2002)) on each track to remove implausible bird locations. We considered a bird to be flying when speed was above 10 km h⁻¹ (Weimerskirch et al. 2002).

Once each track was filtered, we added environmental variables to each GPS location.

Sea surface temperature (SST, °C), 10 meters wind *u* and *v* components (m s⁻¹) and total cloud cover (TCC, %) data were downloaded from Copernicus platform as NetCDF files, extracted from ‘ERA5 hourly data on single levels from 1979 to present’ (Copernicus 2017), a reanalysis of the global climate data (spatial resolution: 0.25 degrees per 0.25 degrees grid, temporal resolution: 1 h).

Wind direction and speed were derived using following formulas (Ostrenga 2019):

$$\text{wind}_{\text{speed}} = \sqrt{\bar{u}^2 + \bar{v}^2}$$

$$\text{wind}_{\text{direction}} = \tan^{-1}(\bar{v}, \bar{u}) \times \frac{180}{\pi} + 180$$

We also added celestial parameters:

- Sun presence was calculated with ‘TripEstimation’ R package (Sumner et al. 2009) using respectively ‘*elevation()*’ and ‘*astro()*’.
- Sunrise and sunset time were obtained with ‘suncalc’ R package (Thieurmél and Elmarhraoui 2019) in order to calculate night duration (difference between sunset time and sunrise time for each location) and to identify locations during day, night, civil dawn or dusk (Furness et al. 2018). Dawn was considered to begin when the sun is six degrees below the horizon and ends at sunrise time. Dusk begins at sunset time and ends when the sun is six degrees below the horizon.
- Night duration was calculated for each location with the difference between sunset and sunrise time.
- Moon parameters (presence – when above the horizon –, altitude, illuminated fraction) were extracted with ‘oce’ R package (Kelley et al. 2020) using some outputs of the ‘*moonAngle()*’ function.

These latter parameters were used to establish a new formula to have a better proxy of moon illumination. Indeed, previous

Table 1. Number of loggers deployed on albatrosses each year on the three islands. In brackets the number of usable tracks (n = 141 in total).

Year	Crozet		Kerguelen		Amsterdam		Total per year	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
2017	17 (6)	46 (55)	0	0	0	0	17 (6)	46 (55)
2018	16 (8)	45 (49)	23 (18)	24 (27)	10 (8)	8 (10)	49 (34)	77 (86)
2019	14 (11)	0	14 (14)	0	9 (6)	0	37 (31)	0
Total	47 (25)	91 (104)	37 (32)	24 (27)	19 (14)	8 (10)	103 (71)	123 (141)

studies about the impact of moon illumination on seabirds only used the illuminated fraction of the Moon (Fig. 1a) or the moon phase as a proxy of moon illumination (Phalan et al. 2007, Yamamoto et al. 2008, Regular et al. 2011, Cruz et al. 2013), without taking into account either moon altitude or total cloud cover. It has been recently criticized by Kyba et al. (2020) who indicated that such measures do not provide the real light conditions encountered. In order to precisely measure real illumination at the albatross location, we elaborated a simple formula to have a better proxy of this parameter.

We calculated moon illumination taking into account illuminated fraction of the Moon (between 0 and 1), moon altitude (angle between -90° and $+90^\circ$) and moon presence (0 or 1) as advised by Kyba et al. (2020).

Therefore, we used the following formula that considers the moon illumination to be maximal when the Moon reaches her zenith ($\text{moon}_{\text{altitude}} = +90^\circ$) (Fig. 1b):

$$\text{moon}_{\text{illumination}} = \text{moon}_{\text{presence}} \times \sin\left(\text{moon}_{\text{altitude}} \times \frac{\pi}{180}\right) \times \text{moon}_{\text{illuminated fraction}}$$

However, even if the previous formula should increase the precision of the real moon illumination received on earth at a given place and time, it doesn't take into account the impact of cloud cover. With the highly precise open source data set online on Copernicus platform, we elaborated a formula to consider the effects of the total cloud cover (TCC), using diffusion and transmission coefficient (Fig. 1c):

$$\text{moon illumination}_{\text{calculated}} = \text{moon}_{\text{illumination}} \times k_{\text{diffusion}} \times k_{\text{transmission}} + \text{moon}_{\text{illumination}} \times (1 - k_{\text{diffusion}}) \times k_{\text{transmission}}$$

$k_{\text{diffusion}} = 0.9 \times \text{TCC} + 0.1$. The more clouds there are the more diffusion there is, but with a TCC of 0 there is still a bit of diffusion.

$k_{\text{transmission}} = (1 - \text{TCC}) \times 0.95 + 0.05$. It considers that a total cloud cover of one almost annihilates transmission, leaving only a bit of light passing through.

This new formula generates a proxy of moon illumination which is generally lower compared to standard estimates of moon illumination (Fig. 1): Moon illumination modulated by total cloud cover and moon altitude (student test, $t = -106.18$, $df = 62\ 341$, $p\text{-value} < 2.2e-16$) and also lower than moon illumination using only the illuminated fraction of the satellite (student test, $t = 150.02$, $df = 54\ 330$, $p\text{-value} < 2.2e-16$).

Analyses

For relative comparison purposes, we created a spatial point class object for both age categories of bird from both species with 'SpatialPointsDataFrame()' R function (from 'sp' R package). From these, we produced kernel utilization distributions (UDs 50% and 90%), using the 'kernelUD()' R function from 'adehabitatHR' R package (smoothing parameters, $h = 1$ degree). We then calculated overlaps on UD 90% between both species and age categories with 'kerneloverlap()' R function (Sanchez et al. 2018). This

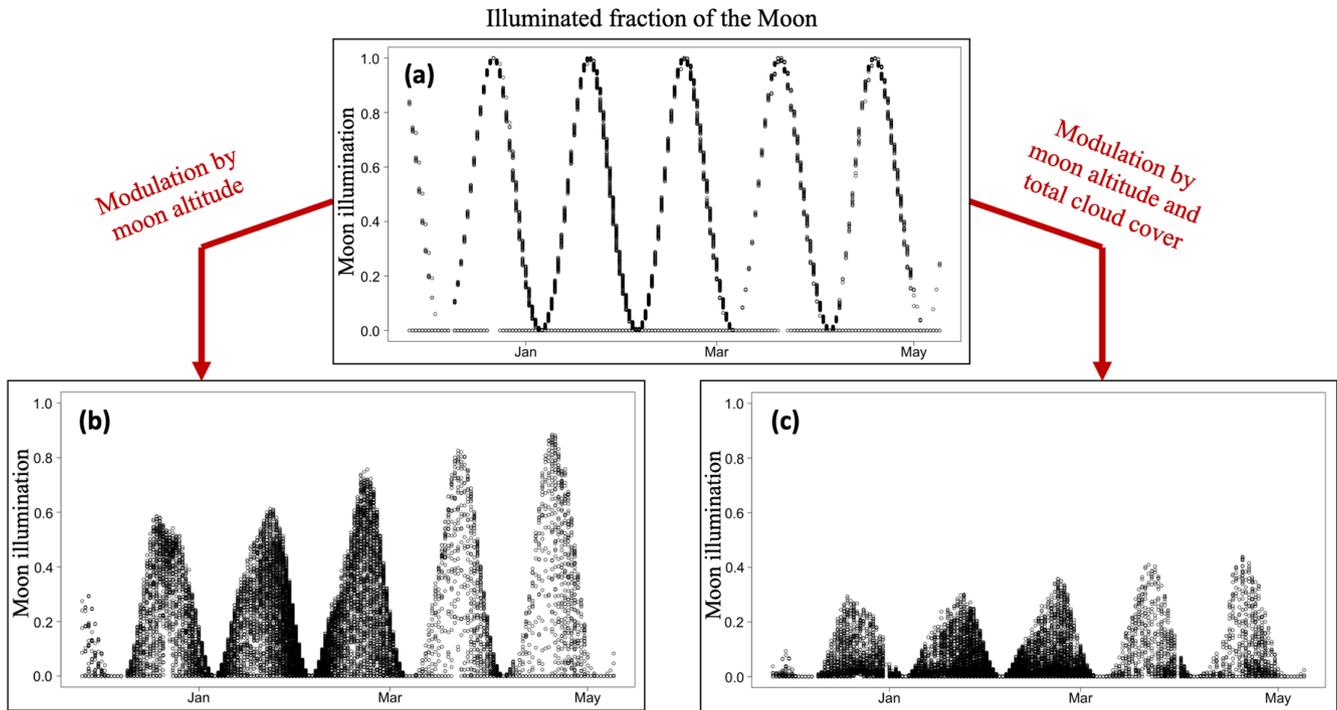


Figure 1. Differences in formula impacts on moon illumination proxy. One dot represents the illumination received by an albatross during one night location within the 2018–2019 season.

function calculates a ratio of superposition between one kernel distribution and another.

In order to study the foraging and movement ecology of both species of albatrosses we estimated two parameters of bird flight behavior. For these, the shortest distance between two locations (i.e. the great-circle distance) was calculated using 'distCosine()' function from 'geosphere' R package.

- 1) For each day, we calculated the proportion of time spent in flight during daylight, at night, at dusk and at dawn which is the number of locations with the bird flying over the total number of locations during the defined period.
- 2) For each location, we calculated the speed of the bird when flying. Also known as ground speed, it is the distance between the previous and the current location divided by the interval of time between both locations. At a one-hour scale, this parameter is not the absolute value representative of the real speed between two locations. Indeed, birds are not going in straight line each time they are flying. However, relatively, we can evaluate differences in the foraging and movement behaviour between groups of albatrosses using this parameter (De Grissac et al. 2016).

From these parameters, we performed analyses using generalized linear models (GLM), linear (LMM) and generalized linear mixed models (GLMM ('lme4' R package (Bates et al. 2015))). Distribution of the two flight parameters were: binomial for time spent in flight and negative binomial for speed.

To test our first hypothesis, change over time of juvenile flight behavior, we fitted GLMMs. One model was performed for each flight parameter, for both groups of juveniles, from each species and by day and night (i.e. 8 models (Table 3)). The random structure was established by AIC selection between two random factors: ring number (for individual identification) and date of departure. In particular, we tested the effect of individual identification on the slope to evaluate the effect of logger duration on the total model. The covariate was the number of days or nights since departure.

We tested whether the response was linear or logarithmic (by log-transforming the covariate). When a logarithmic growth was significant, we modelled the equation by computing three commonly used growth curves (Ricklefs 1983, Benharzallah et al. 2015): Von Bertalanffy, Gompertz and logistic equations (Ricklefs 1983). We chose the one that fitted best to the data by AIC selection and extracted two parameters from it: the threshold and the time to reach it.

From these models, we explored our third hypothesis on the effect of light availability at night by adding the proxy of moon illumination as a covariate to the GLMMs representing night flight behaviour of juveniles. Again, we tested whether the response to this proxy was linear or logarithmic. For adults, we performed GLMMs for each flight parameter with moon illumination as covariate and ring number as random factor.

After having studied the evolution of both flight parameters over time and change of these latter with moon

illumination, we compared the value of each flight parameter between each category of albatrosses with LMMs and GLMMs. We studied:

- 1/ The difference between juveniles and adults (covariate = 'age', Table 3) – Hypothesis 1.
- 2/ The difference between day and night for each group of albatrosses (covariate = 'day_night', Table 4) – Hypothesis 2.
- 3/ The difference between both species' individuals of similar ages (covariate = 'species', Table 5). – Hypothesis 4.

Individual identification was always used as random factor.

Finally, to examine our last hypothesis concerning the diel activity pattern of each group of birds, we used the ratio of time spent in flight throughout the day. First, each location was characterized as a proportion of day or night duration centered on sunrise. Therefore, a whole day is represented by values between -1 and $+1$ with 0 being the sunrise location.

For example:

- 1/ A location three hours after sunrise for a day lasting six hours has a value of 0.5 .
- 2/ A location four hours before sunrise for a night lasting twelve hours has a value of -0.33 .

This method is called the 'equinoctial anchoring' presented by Vazquez et al. (2019). It enables us to overcome the issue of different day lengths between all birds foraging in different habitats under different latitudes. Then, we plotted the data with a 'geom_smooth()' regression ('ggplot2' R package) to observe the pattern.

All data processing and analyses were made under R environment (<www.r-project.org>).

Results

During the study period, we received a total of 116 520 GPS locations from 187 birds. Centurion transmitters were left on adult breeders during one trip at sea, lasting on average for 11 days (Amsterdam albatrosses: 10 days, wandering albatrosses: 11 days). XArgos loggers, because of a technical problem, did not function as long as expected, lasting continuously on average for 41 days (Amsterdam albatrosses: 58 days, wandering albatrosses: 37 days).

Spatial segregation

Juvenile and breeding adult Amsterdam albatrosses were not segregated in space (Fig. 2, Table 2, Supporting information), whereas for wandering albatrosses only 30% of the 90% kernel of juveniles overlapped with those of adults. Breeding adult wandering albatrosses were highly segregated from adult and juvenile Amsterdam albatrosses (Fig. 2, Table 2, Supporting information). The differences in ranges between juveniles wandering albatrosses and Amsterdam albatrosses

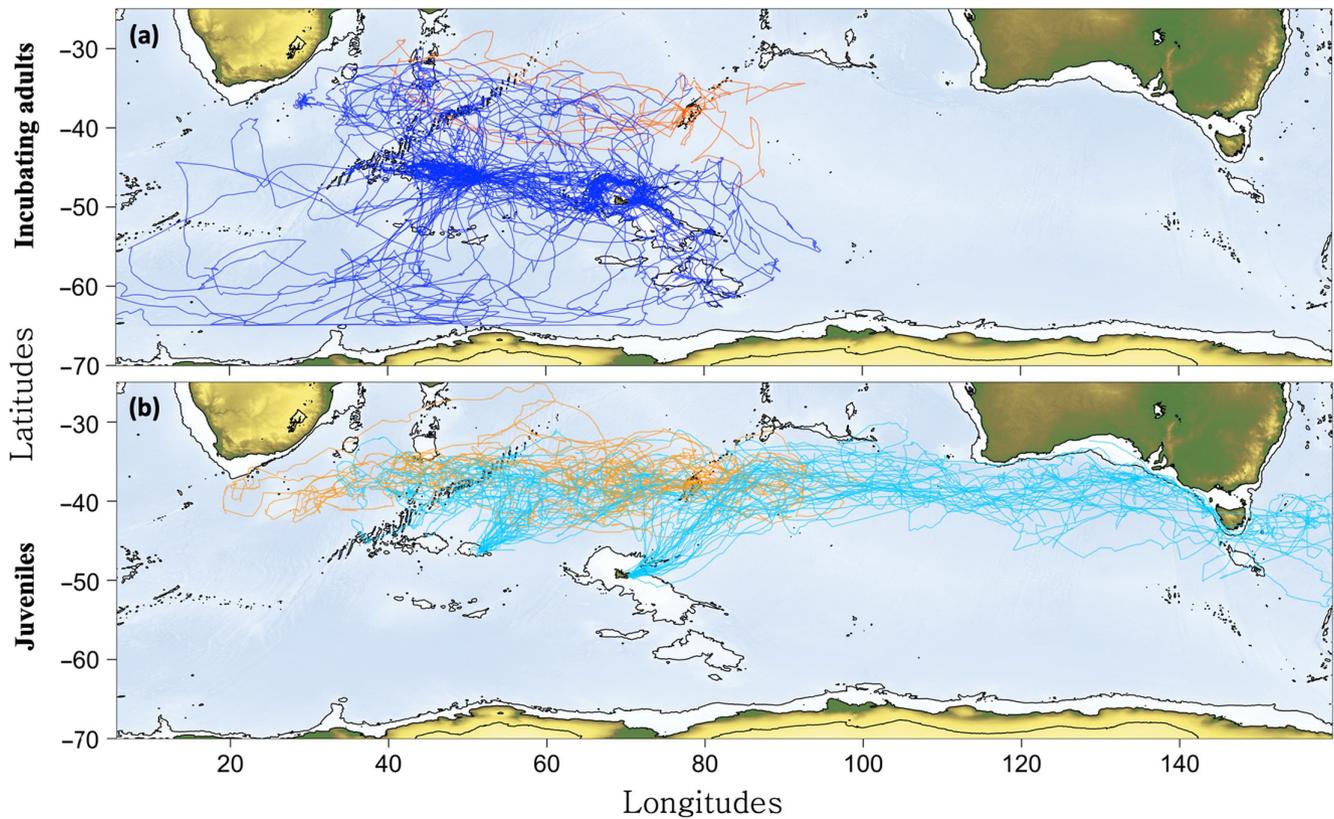


Figure 2. Study area with all the tracks ($n=212$) of both species, Amsterdam albatrosses in orange and wandering albatrosses in blue: (a) adults are on upper map and (b) juveniles are on lower map.

resulted from the eastern movements of juvenile wandering albatrosses toward Australian coasts.

Sea surface temperatures encountered were significantly different between adults of both species (t -test, $t=17.18$, $df=2090.4$, p -value $< 2.2e-16$). Wandering albatrosses forage in sub-Antarctic waters, 10°C colder than tropical and subtropical waters where Amsterdam albatrosses forage. The difference between juveniles of both species was less important but still significant (t -test – $t=155.29$, $df=52885$, p -value $< 2.2e-16$). However, even if the difference was significant between both age classes (t -test – adults: $t=-2.5749$, $df=1820.7$, p -value $=0.01011$ /juveniles: $t=-31.66$, $df=28856$, p -value $< 2.2e-16$), wind speeds encountered by both species were similar with less than 1 km h^{-1} of difference in mean for adults and 3 km h^{-1} for juveniles. Finally, as both species foraged on average at different latitudes, night duration was different, particularly during summer. Night duration was longer for Amsterdam albatrosses than for wandering

albatrosses in both age categories (t -test – adults: $t=250.62$, $df=2602.2$, p -value $< 2.2e-16$ /juveniles: $t=216.36$, $df=21503$, p -value $< 2.2e-16$).

Daily changes in flight behavior of juveniles and comparison with adults

Between both parameters estimated for juveniles, only the ratio of time spent in flight increased significantly with time for both species by day and at night (Table 3, Supporting information). By day, Amsterdam albatrosses reached a threshold, acquired in 41 days, which was not different from the average value of adults. For wandering albatrosses, juveniles reached the same value as adults in 26 days (Supporting information). In both species, the time spent in flight by night was lower for juveniles than for adults. That parameter changed logarithmically for Amsterdam albatrosses and linearly for wandering albatrosses. However,

Table 2. Overlap ratio of 90% kernel for each category of albatrosses. As an example, 0.78 signifies that the range of the juveniles from Amsterdam is overlapped at 78% by the one of Amsterdam adults.

	<i>D. amsterdamensis</i> (Ad.)	<i>D. amsterdamensis</i> (Juv.)	<i>D. exulans</i> (Ad.)	<i>D. exulans</i> (Juv.)
<i>D. amsterdamensis</i> (Ad.)	1.00	0.85	0.48	0.93
<i>D. amsterdamensis</i> (Juv.)	0.78	1.00	0.46	0.90
<i>D. exulans</i> (Ad.)	0.34	0.36	1.00	0.74
<i>D. exulans</i> (Juv.)	0.28	0.29	0.30	1.00

Table 3. Change of flight parameters over time and comparison between adults and juveniles of a same species. (a Night threshold values calculated after to the time necessary to reach a threshold by day.) p-values ** and *** represent $p < 0.01$ and $p < 0.001$.

Flight parameter	Day/night	Change over time			Adults–juveniles comparison			
		Daily evolution	Trend	Pr(> z)	Juveniles' reference value	Time (days) to reach threshold (when change over time)	Adults' reference value	Pr(> z)
Amsterdam albatrosses – <i>Diomedea amsterdamensis</i>								
Ratio time spent in flight	Day	YES	Log	< 2e-16***	0.607 ± 0.488	41	0.733 ± 0.443	0.111
Speed		NO	NA	NA	39.483 ± 29.371	No	38.834 ± 15.594	0.663
Ratio time spent in flight	Night	YES	Log	0.000971***	0.183 ^a ± 0.387 ^a	41 ^a	0.602 ± 0.490	2.81e-05***
Speed		NO	NA	NA	31.610 ± 22.829	No	31.619 ± 12.577	0.194
Wandering albatrosses – <i>Diomedea exulans</i>								
Ratio time spent in flight	Day	YES	Log	< 2e-16***	0.512 ± 0.500	26	0.546 ± 0.498	0.8657
Speed		NO	NA	NA	36.650 ± 24.833	No	37.036 ± 16.904	0.929
Ratio time spent in flight	Night	YES	Linear	1.09e-12***	0.158 ^a ± 0.364 ^a	41 ^a	0.263 ± 0.440	0.00594**
Speed		NO	NA	NA	32.494 ± 24.184	No	30.781 ± 14.724	1.99e-08***

at the end of loggers functioning, juveniles of both species were still increasing their ratio of time spent in flight by night. Therefore, to obtain a reference value for comparison, we used the time necessary to reach a threshold value during daytime.

Flight speed did not change over time in juveniles and was similar to adults' one for both species, except for juvenile wandering albatrosses that had a slower night speed than adults (Table 3, Supporting information).

Day-night comparison and effects of moon illumination

For each group of albatrosses, flight parameters values were significantly lower by night (Table 4). However, when moon illumination was brighter, both parameters were increasing (either linearly or logarithmically) for each group of albatrosses. Only the speed of juvenile wandering albatrosses did not increase with moon illumination (Table 4).

Interspecific comparison

By day or night, for both age classes (juvenile and adults), Amsterdam albatrosses spent more time in flight than wandering albatrosses. Nonetheless, speed was not different by day or night between albatrosses of the same category of age (Table 5).

Diel activity pattern

For all categories of albatrosses, the diel flying activity of each group of albatrosses throughout a day (Fig. 3) was at the highest value just after sunrise (Fig. 3, Supporting information). Later during daylight, after being slightly lower, activity of adults from both species increased again at dusk to attain its lowest value at night (Fig. 3). We observed a similar pattern in juveniles with their ratio of time spent in flight decreasing after the peak around sunrise to be close to zero by night and without peaking at dusk (Fig. 3, Supporting information).

Table 4. Comparison of flight parameters between day and night and the effect of moon illumination by night for each category of birds. p-values *, ** and *** represent respectively $p < 0.05$, $p < 0.01$ and $p < 0.001$.

Group	Flight parameter	Day–night difference		Trend	Effect of moon illumination	
		Estimate	Pr(> z)		Estimate	Pr(> z)
Amsterdam albatrosses – <i>Diomedea amsterdamensis</i>						
Juveniles	Ratio time spent in flight	–2.213	1.6e-07***	Log	0.25476	1.66e-07***
	Speed	–0.34756	7.34e-12***	Log	0.06497	0.00903**
Adults	Ratio time spent in flight	–0.593	2.57e-06***	Log	0.7465	2.06e-11***
	Speed	–0.2968	0.0201*	Linear	41873.989	2.67e-09***
Wandering albatrosses – <i>Diomedea exulans</i>						
Juveniles	Ratio time spent in flight	–1.9716	<2e-16***	Linear	0.11152	0.000419***
	Speed	–0.30513	<2e-16***	Linear	0.006995	0.701
Adults	Ratio time spent in flight	–1.34919	<2e-16***	Log	0.5339	<2e-16***
	Speed	–0.23151	1.99e-08***	Log	0.05881	8.88e-08***

Table 5. Interspecific comparison of birds of the same age category for each flight parameter.

Group	Day/night	Flight parameter	Interspecific comparison		
			Amsterdam albatross value	Wandering albatross value	Pr(> z)
Juveniles	Day	Ratio time spent in flight	0.607 ± 0.488	0.513 ± 0.500	0.029295*
		Speed	39.483 ± 29.371	36.650 ± 24.833	0.186
	Night	Ratio time spent in flight	0.183 ± 0.387	0.158 ± 0.364	0.631
		Speed	31.610 ± 22.829	32.494 ± 24.184	0.859
Adults	Day	Ratio time spent in flight	0.733 ± 0.443	0.546 ± 0.498	0.00262**
		Speed	38.834 ± 15.594	37.036 ± 16.904	0.51
	Night	Ratio time spent in flight	0.602 ± 0.490	0.263 ± 0.440	1.97e-06***
		Speed	31.619 ± 12.577	30.781 ± 14.724	0.267

Discussion

Studying juveniles' foraging and movement ecologies in comparison to adults' performances may enable us to understand the drivers of a higher juvenile mortality (Weimerskirch et al. 1997a, Fay et al. 2015). In this paper, we provided the first comparison of changes in movement and foraging parameters, by day and night, through the first weeks of independence at sea of two closely related species of *Diomedea* albatrosses. This learning period, is a topic of growing interest among seabirds (Yoda et al. 2004, Riote-Lambert and Weimerskirch 2013, Votier et al. 2017, Sherratt and Morand-Ferron 2018, Campioni et al. 2019, Collet et al. 2020, Corbeau et al. 2020).

In our paper we used a different approach to explore this issue by studying either the linear or the logarithmic change over time, by day and night.

We found that the ratio of time spent in flight by juveniles increased over time, by day and night. By day, for both species, it reached a threshold similar to the reference value of adults. Thus, within a few weeks, juveniles become able to fly during an important proportion of the daytime. The fact that juveniles reached a plateau, suggests that they either developed physical maturity or learned how to minimize their energy expenditure through the development of flight efficiency. Both hypotheses have been recently studied on geese (Gatt et al. 2020) and authors showed that the

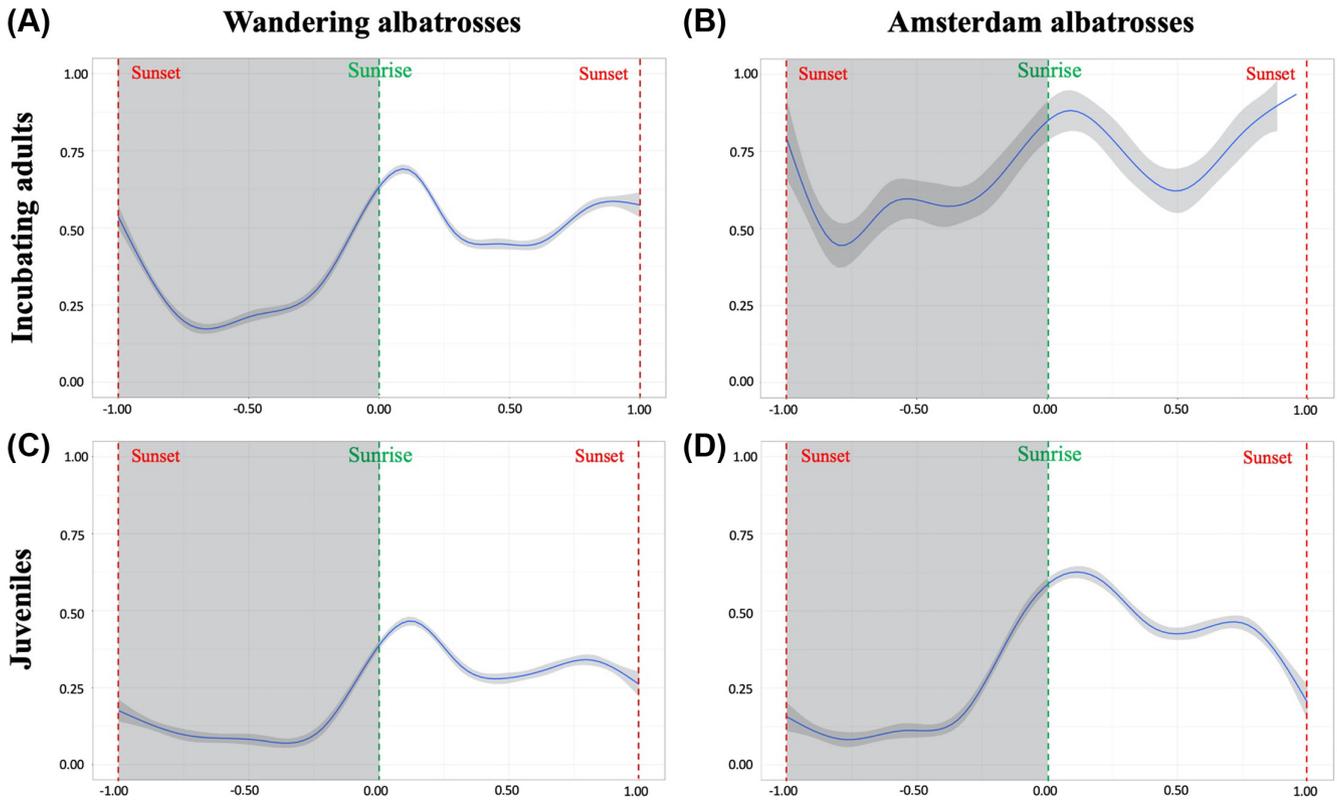


Figure 3. Diel activity pattern of wandering and Amsterdam albatrosses. (a) Incubating adults of wandering albatrosses. (b) Incubating adults of Amsterdam. (c) Juveniles of wandering albatrosses. (d) Juveniles of Amsterdam. Activity is the ratio of time spent in flight between all locations from each group at a given moment of the day. Confidence interval is the 95% level interval computed by ggplot() R function.

'physical development hypothesis' has a more important role in decreasing energy expenditure than the development of flight efficiency. Albatrosses practicing dynamic soaring, this remains to be proven, for example by measuring energy expenditure with heart rate sensors.

Juvenile Amsterdam albatrosses take more time to reach adults' values compared to wandering albatrosses. However, the higher asymptotic value for juvenile Amsterdam albatrosses compared to wandering albatrosses could be an explanation for that difference.

By night, juvenile individuals of both species increased the ratio of time spent in flight without reaching a plateau. Nonetheless, loggers did not function as long as expected and stopped before birds potentially reached this threshold. In each case, flying activity of juveniles is lower than the one of incubating adults leading us to reject our second hypothesis assuming that juveniles have a higher night activity to compensate a lower foraging efficiency during daylight.

The other studied parameter, speed, did not change over time by day or night and was identical between both age classes of a same species. In albatrosses, flight speed is highly dependent on wind utilization (Alerstam et al. 1993, Reinke et al. 1998, Richardson et al. 2018). Therefore, juveniles could be using winds optimally as soon as they leave their nest, which has been previously suggested for wandering albatrosses (Riotte-Lambert and Weimerskirch 2013) but not for Amsterdam albatrosses.

Exploring night activity allowed us to investigate a poorly explored topic for animals and especially for juvenile seabirds (Kronfeld-Schor et al. 2013). Juvenile seabirds' night behavior has, to our knowledge, never been explored before and, for our two targeted species, only been studied in adult wandering albatrosses (Weimerskirch and Wilson 1992, Weimerskirch et al. 1997b, Phalan et al. 2007, Nevitt et al. 2008). These studies show that, like other albatrosses, wandering albatrosses have a reduced activity by night. Our results support this observation. For each of the four groups (juveniles and adults of both species) we compared day and night activity values for both parameters. Ratio of time spent in flight and speed were lower by night than by day.

There are several assumptions to explain why albatrosses spend less time in flight by night than by day which are reviewed by Phalan et al. (2007). First, foraging efficiency could be reduced because it is harder to fly, detect and catch prey at low light levels. Second, albatrosses may use another feeding strategy, the 'sit-and-wait' technique at night (Weimerskirch et al. 1997b). Based on the diel vertical migration (DVM), this hypothesis is explained by a higher concentration of prey at the surface by night (Gliwicz 1986b, Luecke and Wurtsbaugh 1993). Then the balance between energy consumption and energy gain seems better for birds when sitting-and-waiting for smaller and less energetic prey than flying in the dark for bigger prey – similar to the ones they catch during the day – (Weimerskirch et al. 1997b).

Our analyses support both hypotheses because with reduced light, both species of albatrosses reduce their flight activity to sit on water. However, seabirds' night activity increases with

moon illumination for many species (Yamamoto et al. 2008, Pinet et al. 2011, Regular et al. 2011, Cruz et al. 2013) and also for wandering albatrosses (Weimerskirch et al. 1997b, Phalan et al. 2007, Nevitt et al. 2008, Mackley et al. 2010). In our study we have examined the effect of a more precise proxy of moon illumination on the activity of both studied species. This proxy considers the altitude of the Moon and the cloud cover at the location date and hour. Commonly, the illuminated fraction of the Moon serves as proxy of moon illumination. It is a 29-day cycle through which the amplitude of the illumination ranges from 0 during new moon to 1 in full moon. Our formula keeps the same cycle, following the classical curve but with a lower amplitude because birds' locations are not often during the Moon zenith and cloud cover was very high during the study period (mean of total cloud cover by night from our data = 73%). Therefore, we have a better measure of the real illumination encountered by the birds and can measure more precisely its impact on flight behavior. We assume this proxy, inspired by the technique used in a recent study (Portugal et al. 2019), to be closer to reality than proxies used in other ecological studies. Correlated with a brighter moon illumination, the speed and the ratio of time spent in flight by night increased for both species and both age categories. Only the speed of juveniles of wandering albatross did not, probably due to the high standard deviation of the parameter. Those results are supporting the hypothesis about the impact of darkness on albatrosses' activity which could be explained by a better visual acuity of individuals.

Therefore, with parameters studied continuously during 24 hours we were able to explore the diel activity pattern and particularly the flying activity during dawn and dusk which has little been studied in albatrosses and in seabirds more generally.

For adults and juveniles of both species we found a peak of activity at dawn. With DVM happening at night, prey availability must be higher during duskiess hours than during daylight ones, as indicated by the increased activity of many seabirds observed behind long-liners at dusk and dawn (Murray et al. 1993). We observed a peak of activity at dusk only for adult birds. In contrast, juveniles flying activity seemed to decrease progressively during the day to stop after sunset. We can therefore assume that the second activity peak observed in adults might be acquired later during the immature phase. A second hypothesis is that energy requirements are higher for adults than for juveniles, therefore incubating birds should spend more time foraging than juvenile ones.

From both studied parameters only the ratio of time spent in flight differed between adults of both species: Amsterdam albatrosses spent more time in flight than wandering albatrosses by day and night. Amsterdam albatrosses have very high values of time spent in flight at night and during the day (both above 60%) whereas wandering albatrosses spent less than 60% of the time flying by day and around 30% by night, suggesting different feeding strategies between the two species.

By day, wandering albatrosses are known to forage over extensive distance, detecting prey visually or by olfaction

(Nevitt et al. 2008). It is called the ‘foraging-in-flight’ strategy which is the lowest energy consuming feeding strategy for wandering albatrosses (Weimerskirch et al. 1997b). However, this strategy tends to change when birds are incubating, with birds spending more time on water (Phalan et al. 2007, Louzao et al. 2014) leading to a more important utilization of the ‘sit-and-wait’ technique. This technique is used at night by wandering albatrosses when they spend around 70% of their time on water. (Weimerskirch et al. 1997b). It appears to be efficient in productive area where DVM is important (Weimerskirch et al. 2005).

Incubating Amsterdam albatrosses spent 75% of their time flying by day and around 62% by night, twice the value of wandering albatrosses. Foraging activity and especially nocturnal activity has been proven to change in accordance to SST for a same species with populations foraging in different habitats (Dias et al. 2012). Amsterdam albatrosses live in a less productive area with a lower DVM compared to wandering albatrosses. Therefore, the ‘sit-and-wait’ technique might be not efficient enough to compensate the energy allocated for the incubation and to search for food. Amsterdam albatrosses could spend more time searching for scarce prey in poorer subtropical waters, like their counterparts from Hawaii island do (Fernández and Anderson 2000). However, another aspect may explain such an important night activity: predator avoidance. It has already been proved that marine predators such as sharks feed on seabirds and albatrosses (Fisher 1975). Since they are also visual predators, bright light conditions enable them to see more easily what happens on the water surface, which has consequences on prey’ activity. Most of shark species live in warm sea temperature, which might increase the time spent in flight for Amsterdam albatrosses, especially under bright moon. A last hypothesis could be that visual acuity of Amsterdam albatrosses is better at night than wandering albatrosses, which would allow them to fly more easily in dark conditions.

Food and foraging strategy of Amsterdam albatross was unknown: we show here that it differs from wandering albatross in the time spent in flight per day. However, during this flying time, speed is not different between species, neither for juveniles nor for adults suggesting that flying behaviour is the same. This might be explained by the relatively close anatomy of both species and a similar use of the wind conditions, which are quasi-identical between foraging areas of both species.

Conclusion

In conclusion, juvenile albatrosses acquired several movement capacities through their early life, a critical period with high mortality. The time of acquirement and foraging strategy, by day or night, differed between species possibly in relation to prey availability. The latter has to be further examined, particularly in subtropical areas where the Amsterdam albatrosses (until recently a critically endangered species) forage, but the results already underline the importance of environmental and trophic conditions to understand how seabirds and especially juveniles behave. With the development of

new technologies deployed on marine predators and the emergence of more comprehensive and complete datasets exploring the influence of biotic and abiotic conditions, more precise studies on the ontogeny of movement and foraging behaviour are now possible and needed.

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Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.10.1111/jav.02597>> (Pajot et al. 2020).

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