ACTIVITY AND MIGRATION OF CORY'S SHEARWATER

Master thesis

Santi Guallar

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Contents

BACKGROUND AND WORK DESCRIPTION

Migration, molt, reproduction and wintering, the main life-history stages of a seabird are irreversible and fit a routine with a circannual periodicity. For example, reproduction takes place more or less on the same dates year after year, and molt usually starts after reproduction and not the other way around. Transition from a stage to the next and their respective durations depend on a combination of endogenous and exogenous factors that have been optimized during each species' evolution (McNamara and Houston 2008). Each stage entails tasks which involve a series of behavioral changes, and a different activity pattern characterizes each of these behaviors.

Studies on factors that trigger and control these changes in animals have been conducted since the early XXth century (Szymanzki 1918), and by the end of the century it was already discovered a gene that regulates endogenous rhythms in vertebrates (Vitaterna et al 1994).

Environmental cues are known to exert a strong influence on avian activity either directly or indirectly. Among these, photoperiod has been investigated for many decades (*e.g.* Gwinner 1977, Noskov and Rymkevich 1982, Wikelski et al 2000), and, for instance, gonadal maturation (Jacobs and Wingfield 2000) and onset of molt (Dawson 2008) are two well known processes in which drastic changes of behavior are controlled by photoperiod. Other cues that may trigger behavioral changes are social stimulus, temperature and lunar cycle.

Seabirds are animals that rely on visual cues to forage; therefore, light has a strong effect on their activity. The main source of natural light is sunlight, although it is not the only source: moonlight is very important in the night time. The lunar influence on the behavior of seabirds has been relatively poorly documented. For example, Moon phase affects nest attendance patterns (Mougeot and Bretagnolle 2000) and foraging behavior (Phalan et al 2007).

Recent advances in electronic technology and particularly the development of miniaturized geolocator devices have made possible for the first time to "*see the world through the seabirds' eyes*" (Burger and Shaffer 2008). Recent works based on geolocator data have shown that seabirds' activity increases with Moon phase during the non-reproductive period (Yamamoto et al 2008, Mackley et al 2010). Pinet et al (2011) have shown that the behavior of another seabird species is modulated by both photoperiod and Moon phase throughout its annual cycle.

In this work, I describe some of the features that characterize the activity and migration of a seabird Cory's shearwater *Calonectris diomedea* during approximately one year. I also explore the factors that likely shape the resulting patterns and, particularly, its periodicity. To achieve these objectives, I have principally used time series and regression analysis. Time series analysis is an array of techniques that take into account the correlational structure between data to obtain the model that best fits them, and thus make more accurate predictions. Its use here is, after Hart et al (2010) and Pinet et al (2011) works, one of the first applications to the analysis of logger data in seabirds.

Recent investigations on seabird activity have already shown the influence of Moon and photoperiod. To my knowledge, this is the first time in which flight activity has been shown to be also influenced by the lunar phase and the number of hours of moonlight during the natural night. An intriguing finding of this work is the lunar periodicity that pervades the annual cycle of this species.

Reduced sample size has precluded the generation of reliable models to explore the factors that may influence onset of migration and arrival at the breeding and wintering areas. Males average earlier onset of migrations and arrival at their final destinations; however, differences are non-significant. Regardless of which sex starts migrating earlier, Cory's Shearwaters set the onset of its post-nuptial migration after the end of the African summer monsoon, as already shown by Felicísimo et al (2008). During this monsoon the prevailing winds "block" the passage of the equatorial belt, which seems to be a desert to seabirds, and therefore try to fly through as fast as they can.

Pre-nuptial migration averages shorter than the post-nuptial one although differences are non-significant. The factors behind this are unclear.

Overall, this investigation provides some interesting results and leaves open questions that merit further study.

MEET CORY’S SHEARWATER

This section provides relevant information on the organism of study, and it is meant to understand and interpret this work in its underlying biological context.

Cory’s shearwater is the largest of the European shearwaters, with an average wingspan of 125 cm and a weight of 600-800 g (*C. d. borealis*, mean size ± SD = 126.30 ± 5.33 cm, n = 127; mean mass ± SD = 785.80 ± 86.98 g, n = 771; Reyes-González and González-Solís 2012). It has rounded head, long wings and short tail. All ages show dull plumage, grayish brown on the upperparts and head, almost entirely white underparts, except the outer edge of the wings, which is dark. The upper tail coverts often form a narrow white band which separates tail and rump. Cory’s shearwaters have a stout and long yellowish bill with blackish tip, which very patent nostrils; legs are pinkish (figures 1, 2).

Figure 1. ***Calonectris diomedea borealis*** **off Pico (Azores) on 12 June 2009. ´ Gerard Visser**

There is a slight but clear sexual dimorphism in size within each breeding pair, with males being on average 10% heavier than females (Navarro et al 2008). The width and length of the head and bill are the characters that best discriminate both sexes, with higher values in males (Lo Valvo 2001). Also, the upper tip of the bill is more developed in males (Navarro et al 2008).

Figure 2. ***Calonectris diomedea diomedea*** **off Menorca on 17 July 2008. ´ Juan J Bazán**

Cory's Shearwater has the typical seabird morphology, with long slender wings adapted to make the most of the sea surface winds (González-Solís et al 2009). Its flight strategy is based on long glide sequences combined with sequences of active flapping, in which increases the energy consumption considerably. This flight pattern varies with wind speed although the bird always flies near the sea surface: with increasing wind speed decreases the frequency and duration of flapping flight and increases distance from the surface (Paiva et al 2010).

Cory's shearwater is a pelagic seabird that exclusively breeds on islands of the northeast Atlantic Ocean (subspecies *C. d. borealis*) and the Mediterranean Sea (subspecies *C. d. diomedea*) between 15 and 40°N and 28 and 33°W, concretely on Azores, Madeira, Selvagem, the Canaries and the Balearics (Bauer and von Glutz Blotzheim 1987). Its main wintering areas are located at the confluence of the Brazil and Malvinas Currents on the continental shelf off the coast of Uruguay and southern Brazil, in the Canary Current off the coast of Western Sahara, Mauritania and Senegal, and in the Benguela and Agulhas Currents from the waters off Namibia to Mozambique Channel and the Indian Ocean. Therefore, most individuals are trans-equatorial migrants which carry out loop-like migrations once a year (figure 3).

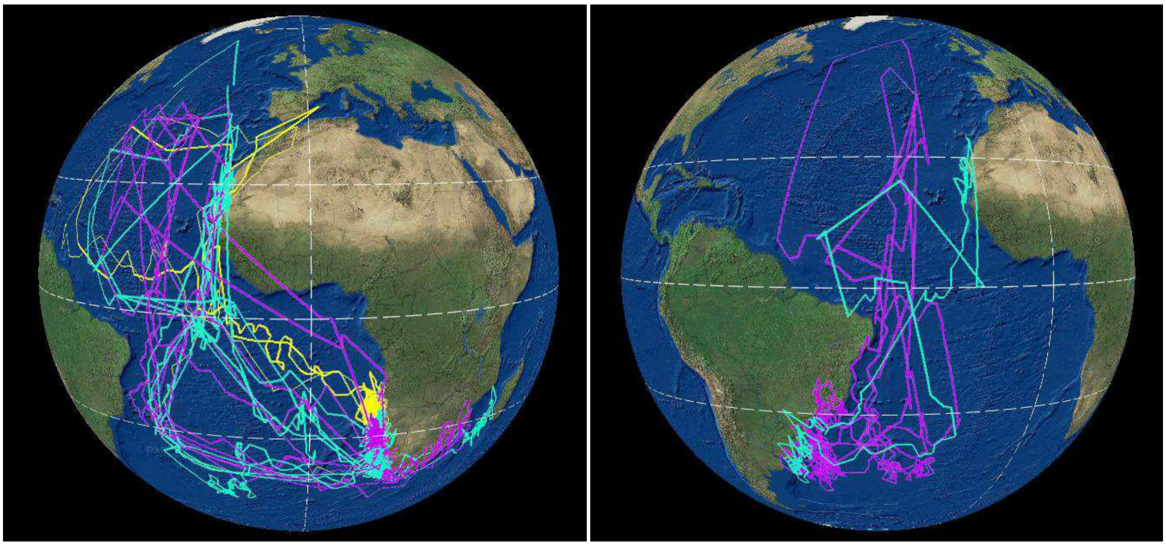

Figure 3. Migratory routes of five individuals which wintered in the southern Atlantic and Indian Oceans (from González-Solís et al 2007).

Cory's Shearwater lives at sea, mostly exploiting neritic zones on the continental shelves but also some oceanic areas, coming ashore only during the reproductive period. It uses warm and temperate waters of the subtropical North Atlantic and the Mediterranean. They are often associated with areas of high biological productivity and ocean fronts, emerging areas of deep water, or extensive continental shelves where prey on small surface animals, mainly small epipelagic fish, but also cephalopods and crustaceans.

Cory’s Shearwater is essentially a diurnal species, which invests much more time foraging during day time, while resting on the water most of the night time (Catry et al 2011). However, it is believed to be active at night, especially in moonlit nights during migration (Reyes-González and González-Solís 2012). In the vicinity of the breeding colonies is largely nocturnal and only enters the nest at night, apparently to avoid predators.

Arrival in the breeding grounds begins in late February and early March, when large groups of individuals come near the colonies (Thibault et al 1997). A few weeks later there is an exodus from the colony that lasts around 20 days. During this period the colony is timely visited by males, always at night, which defend their caves of conspecifics until the female comes to lay. During this pre-laying period females seldom visit the colony (Jouanin et al 2001).

Females lay one single egg in late May or early June, immediately after their return to the colony (Ramos et al 2003). The incubation period spans seven to eight weeks, in which both members of the couple take long bouts (sometimes longer than one week; Bauer and von Glutz Blotzheim 1987). The juveniles fledge 12 to 14 weeks after hatching, in late September and October (Bauer and von Glutz Blotzheim 1987).

GEOLOCATORS

This section is largely based on excerpts from Fox (2010). It is meant to provide the basics to understand the nature of the data used.

Obtaining new information on the natural world involves direct observation, measurement and experimentation. However, this can be challenging for species that are cryptic, rare or impossible to track continuously and directly. As a result, information on the life history, behavior, physiology, and ecology of many animals is scant or non-existent. Bio-loggers constitute a way around this problem; provide basic knowledge on the function of free-ranging organisms that can be useful to manage and conserve species and their habitats and to mitigate human impacts.

"*The scientific field of bio-logging has existed for many years, but recent advances in electronic miniaturization and digital information processing and storage are providing new insights into the hidden lives of animals that can only be studied vicariously, that is, indirectly through the use of technology. Bio-logging generally involves an animal- borne instrument that monitors or records aspects of an animal's biology (e.g. behavior, movements, and physiology) and its environment. For example, bio-logging instruments can record video or still images of animal behavior and record data from a variety of sensors that monitor location and locomotion (three-dimensional movement), physiology (body temperature, heart rate, blood oxygen concentration), and environmental variables (ambient temperature, light level, oxygen concentration, salinity, sound). As bio-loggers become smaller and more data rich, our understanding of and capability to predict how animals function and interact with their environment grow larger*" (Davis 2008).

The geolocator is a logger equipped with a battery, an in-built microprocessor, a clock and a memory for data storage. It is encapsulated in a clear, water resistant package, with two external terminals for command and data transfers. The whole piece is mounted onto a plastic ring and attached on the leg of the bird. The aim of any attachment is to be of minimum size and weight, to cause as little danger to the tagged animal as possible and not to affect its behavior. It is paramount that the active part of the light sensor faces away from the body of the animal and is not shaded.

The loggers deployed to the birds in the sample were Mk 4, which take a light level reading at one-minute intervals and, from those, saves to memory the maximum light measurement every recording interval (ten minutes). The value recorded at the end of each 10-minute period ranges from zero (minimum light sensitivity) to 64 (maximum light sensitivity).

Light level geolocation is the calculation of position from ambient light level readings with reference to time, and is a highly effective technique for tracking long distance migratory species. After data download, decompressed data are processed using special software to estimate position: latitude from day/night length, and longitude from the absolute time of local midday/midnight. The accuracy of this technique is affected by a number of factors including season, latitude, cloud cover, interference from artificial light sources, changes in sensor orientation, etc. For these reasons, an average error ± SD of no better than 185 ± 115 km should be expected for a flying seabird. In addition, for two or three weeks around each equinox, when day length is approximately equal everywhere, the calculation of latitude is unreliable or impossible (longitude is unaffected by equinox) with threshold level geolocation. These errors will affect tremendously any calculation that depends on position, as moonrise/moonset and night-Moon overlap estimates.

Mk 4 loggers also record wet/dry information. This is achieved by measuring conductivity; hence the wet state will only be recorded if the water is salty. Mk 4 sample for wet/dry every 3 seconds and make a record of the total number of samples wet every 10 minutes. Given the sampling interval of 3 seconds, the value recorded at the end of each 10 minute period ranges from zero (always dry) to 200 (always wet).

Shading, cloud and fog are thought to be the main uncontrollable sources of error. The intense artificial light of industrial line-fishing areas causes interference. Location fixing will only be possible when there is a daylight period and a dark night period within any 24 h. The determination of the sunset and sunrise times from the light data is, by far, the most uncertain step in the method and contributes the largest error. This is mostly due to unknown weather and shading conditions. The more these conditions differ from those at the time of the calibration, the larger the error.

After download, logger files should be edited and analyzed with the TransEdit2 program (figure 4) to obtain sunset and sunrise values corresponding to a chosen threshold value. The aim is to match the threshold value to a Sun elevation angle of about –5 degrees (when the light level is changing most rapidly and the Sun is still below the horizon). Unfortunately, data are usually far from ideal and need further processing. Each individual sunrise and sunset curve should be visually considered for acceptance and an appropriate confidence level applied to it.

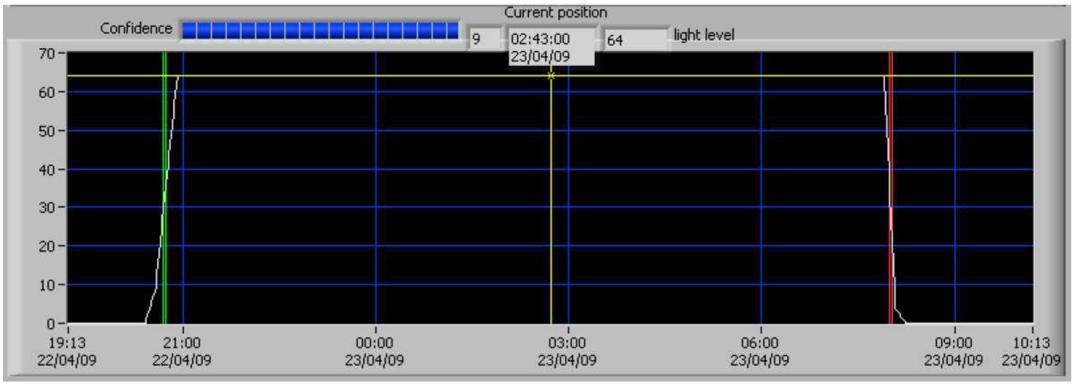

Figure 4. TransEdit2 screenshot showing the process to obtain sunrise and sunset values. Time is on the x axis, light on the y axis. The green and red vertical lines give sunset and sunrise for a threshold fixed at light = 30, respectively.

The Compensate movement box is usually best turned on. Once the transition times have been converted into locations using astronomical formulae, this function goes some way to compensate for bird movement. For example, a bird flying west will see a longer day period than a static target at a point half way through its journey, because it “follows” the Sun. Therefore, the latitude calculation needs to be compensated depending on the change on longitude. The compensation assumes the bird has been moving uniformly between sunrise and sunset (noon data) or sunset and sunrise (midnight data) and is based on the last plotted point (therefore, if the last point has an erroneous longitude value then the next point will be poorly compensated). Fast flying birds moving north or south will also produce some change in day length which will shift the apparent noon position and result in longitude error.

Mk4 loggers have a mass of about 10 g, less than 2% the bird's mass. Igual et al (2005) and Passos et al (2010) showed that light loggers including the Mk 4 neither affect neither the well-being nor the behavior of seabirds.

DEFINITIONS

Numerous concepts and variables will be used in the sections hereafter. Before proceeding, I provide their definitions and how they have been obtained so that their meaning and significance can be understood.

Annual cycle

Life history stages of birds are known to have a circannual periodicity (Gwinner 2003): they largely repeat migration, reproduction and molt every year approximately in the same dates. Here, I refer to four phases of the annual cycle of Cory's Shearwater:

- Breeding: is the season that begins with the birds' arrival into their colonies and finishes with the post-nuptial migration. It encompasses all the reproductive period and its different phases, although it may also include other life history stages such as the onset of plumage molt.
- Post-nuptial migration: is the journey that birds carry out from the breeding to the wintering grounds in the fall.
- Wintering: is the period that spans from the end of the post-nuptial migration until the onset of the pre-nuptial migration. Birds winter in a vast but concrete pelagic area year after year.
- Pre-nuptial migration: is the journey back from the wintering to the breeding grounds that birds carry out in late winter or early spring.

I am treating each one of these phases as homogeneous, although birds engage in different stages within each phase, such as incubation or brooding during the breeding season, which may entail radical changes of behavior, and therefore of activity patterns.

Photoperiod and natural night

The photoperiod is defined as the time elapsed from sunrise until sunset calculated at the local position, and taken from the logger files.

Natural night is defined as the interval of darkness from sunset until the next sunrise, therefore encompassing two consecutive dates.

Activity

At sea activity can be coarsely classified in two categories: flight and foraging.

Activity is one of the primary data obtained by the loggers, and the response variable in most of the analyses. As it has been already mentioned, activity is recorded as a summary of the conductivity sensor every ten minutes, and ranges from 0 (always dry) to 200 (always wet). The resolution of this variable is relatively poor for estimating real number of landings or to estimate bout lengths, for instance.

Flight activity is defined as the time spent off the water. By subtracting the original activity to 200, I obtained more intuitive values: flight activity ranges, then, from 0 (always on/in the water) to 200 (always off the water) for each recorded interval.

Cory's shearwaters are strict pelagic birds except in the breeding season, at the beginning of which males defend their nests, and later on both members of the pair take long bouts in their burrow. Loggers will record continuous activity off the water in this situation, as well as an anomalous daylight pattern because of the bird covering the sensor (figure 5). I have removed the dates in which this false flight activity happened.

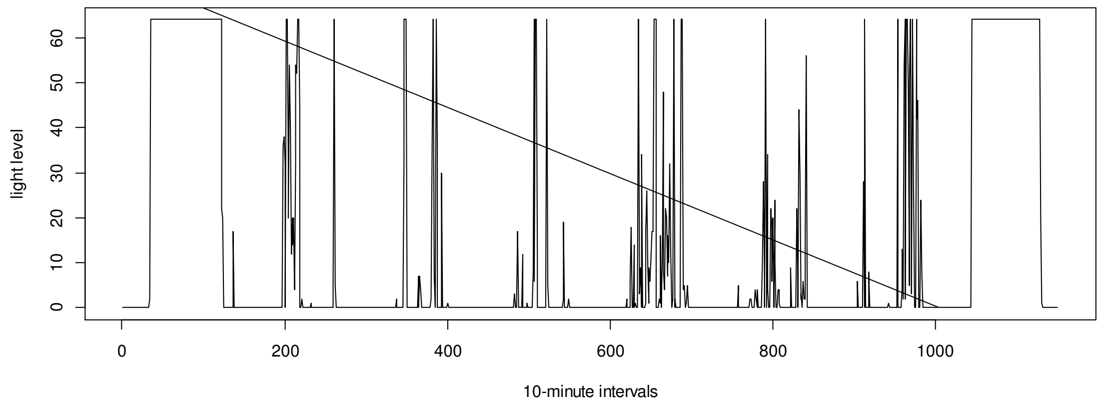

Figure 5. Light record for individual 2298001 from June 15 until June 22. Normal registers show null light levels for the night time and light levels = 64 for the daytime. This bird was incubating during the interval 16-2 June. These days show an anomalous spiky pattern compared to the rectangular one corresponding to non-incubating days.

However, during the pre-laying and the chick-rearing periods birds also enter their burrows exclusively at night, altering also the true activity pattern. This noise has not been removed, although the period and the duration of these visits are relatively short.

I also considered separately diurnal and nocturnal flight activity as the flight activity during daytime and the natural night time, respectively.

For comparative purposes (for instance, between day and night), it is necessary to correct absolute activity values. For this reason, I defined two new metrics of flight activity:

- Relative flight activity is the total diurnal or nocturnal flight activity divided by the total flight activity accumulated between two consecutive sunrises.
- Corrected flight activity is the total diurnal or nocturnal flight activity multiplied by the fraction of daytime or night time in 24 h, respectively.

Landing activity can be interpreted as a proxy of foraging activity, and it is defined as the number of 10-minute intervals (the logger resolution) in which the bird shifts from the wet to the dry state at least once. Thus, it is a count variable that takes values 0 or 1 for each 10-minute interval.

This is a coarse approach to the real landing activity since it is impossible to determine the number of state shifts within each 10-minute interval from the logger summary. One knows for certain that there has been no state change for activity values equal to 0 or 200, and that there has been one state change for activity values equal to 1 or 199. For values from 2 to 198 we can expect an increase of the number of landings in the interval 200 to 100, and then a more or less symmetrical decrease in the interval 100 to 0 depending on factors such as the wind conditions, time of day, phase of the annual cycle, digestive state (‘full’ to ‘hungry’) or density of prey. However, this potential gradient was not considered here since the estimation of the real number of landings from the logger activity record would need additional empirical information.

Lunar phase

Lunar phases are created by changing angles (relative positions) of the Earth, the Moon and the Sun, as the Moon orbits the Earth. Lunar phase is the same at any position on the Earth and it ranges from 0^o (New Moon) to 180^o (Full Moon).

Some additional astronomical basics are needed to understand and interpret the results associated to lunar phase and lunar month.

A synodic month is defined as the average time between new moons and has been observed to be 29.53059 days (29 days, 12 hours, 44 minutes, 2.8 seconds) long. A new moon or a full moon happens when the Moon crosses the plane that is perpendicular to the Earth's orbital plane and passes through the centers of the Earth and the Sun. Interestingly, the Moon finishes its orbit around the Earth in 27.32166 days, but it has not finished a full cycle until it reaches the point in its orbit where the Sun is in the same position (sidereal month). A synodic month is longer than a sidereal month because the Earth-Moon system is orbiting the Sun in the same direction as the Moon is orbiting the Earth. Therefore, the Sun appears to move with respect to the stars, and it takes about 2.2 days longer for the Moon to return to the apparent position of the Sun.

Night-Moon overlap

Night-Moon overlap is the number of hours of moonlight during the natural night. In general there is a positive correlation between the lunar phase and the night-Moon overlap, *i.e.* when lunar phase is increasing from new to full Moon, the Moon tends to be more hours visible during the night time.

DATASET

Basic information on each bird identity is being linked to the logger primary data and to one environmental cue (Moon phase) with the aim to develop the final dataset that has been used in this work.

Basic information of the bird sample

The dataset is based on 20 breeding birds from the Veneguera colony in Gran Canaria captured in June and July 2007, which were deployed with Mk 4 loggers for approximately one year. The basic information of this sample (table 1) is:

- Bird identity: number reference of the metal band attached onto one leg with which they are individually marked
- Sex
- Deployment and recovery dates of the logger attached to each individual.

Logger data

The data registered by the logger consist of time, conductivity and light measurements. TransEdit2 software allows the estimation of other variables, of which I took two geographical positions per date, and the dusk and dawn times. These data are further elaborated to obtain the photoperiod, and the natural night (see Definitions).

Phenology data

Initial dates for the four principal events that divide the individual's annual cycle are also estimated from logger data (table 1).

Arrival at the breeding colonies is estimated as the first day that the bird is anew within the home range of its breeding colony.

Arrival at the wintering area is estimated as the first day that the bird enters the core area of its own wintering range, as defined by the positions of the same birds during the wintering period subsequent to the arrival.

Commencement of pre-nuptial and post-nuptial migration is estimated as the first day in which the bird is out of its own wintering range or out of the home range of its breeding colony, respectively.

Individual	Sex	Deployed	Recovered	Post-nuptial	Wintering	Pre-nuptial	Breeding
2196001	1	20/07/07	01/05/08	19/11/07	05/12/07	20/02/08	17/03/08
2201001	2	18/06/07	01/05/08	28/11/07	31/12/07	09/02/08	14/03/08
2202001	2	21/07/07	28/04/08	15/11/07	04/12/07	14/02/08	15/03/08
2208001	2	25/07/07	29/04/08	22/11/07	02/12/07	25/02/08	30/03/08
2276001	2	16/06/07	01/05/08	13/11/07	01/12/07	14/02/08	10/03/08
2278001	1	16/07/07	25/04/08	30/10/07	27/11/07	13/02/08	29/02/08
2282001	1	20/07/07	01/05/08	06/12/07	24/01/08	16/03/08	06/04/08
2285001	1	20/07/07	01/05/08	19/11/07	06/12/07	18/02/08	04/03/08
2287001	2	23/07/07	30/04/08	21/11/07	04/12/07	13/02/08	29/02/08
2288001	2	25/07/07	30/04/08	20/11/07	16/12/07	20/03/08	11/04/08
2290001	2	20/07/07	28/04/08	13/11/07	04/12/07	21/02/08	17/03/08
2291001	1	16/07/07	30/04/08	21/11/07	15/12/07	06/03/08	22/03/08
2292001	1	16/07/07	28/04/08	10/11/07	03/12/07	05/02/08	16/02/08
2294001	2	25/07/07	20/07/08	02/12/07	30/12/07	17/02/08	04/03/08
2296001	2	24/07/07	27/04/08	20/11/07	17/12/07	03/03/08	29/03/08
2297001	1	16/07/07	26/04/08	11/11/07	06/12/07	08/02/08	19/02/08
2298001	2	20/07/07	21/07/08	01/12/07	30/12/07	19/02/08	18/03/08
2299001	1	16/07/07	26/04/08	04/11/07	02/12/07	03/02/08	21/02/08
2300001	1	20/07/07	29/04/08	18/11/07	13/12/07	29/02/08	10/03/08
2303001	1	16/07/07	02/05/08	14/11/07	05/12/07	21/02/08	16/03/08

Table 1. Basic information and phenology data used in this work.

Moon data

Moon data have been obtained from The Institut de Mécanique Céleste et de Calcul des Éphémérides (IMCCE) and downloaded from:

http://www.imcce.fr/fr/ephemerides/formulaire/form_ephepos.php

Moonrise and moonset varies with latitude and longitude, and calculations require a complex algorithm. A calculator of moonrise and moonset is implemented in package moonsun in R. The instruction to obtain them is easily applied as a function using date and position:

```
f= function(M){options( latitude = M[1], longitude = M[2] )
as.gmt( moon.rst( jday = jd( M[5], M[4], M[3] ) ) )}
```

From moonrise and moonset can be derived the night-Moon overlap (see Definitions).

Time data

All time data are referred to the Greenwich meridian time (GMT).

Final dataset

I removed records from the complete dataset corresponding to the date of deployment and before it, and the records corresponding to the date of recovery and after it. I also removed the dates in which individuals were inferred to be incubating , as indicated by anomalies in their light record. The latter were defined as dates from May, June and July (the ones in which the incubation is known to happen in this species) for which the mean light value registered during daytime was 90% of the mean daytime light value for the whole period.

DATA TREATMENT AND ANALYSES

Data management, plots and analyses have been carried out with R (The R Foundation for Statistical Computing 2012).

Activity and positional data are quite noisy, they have an oscillating pattern that has to be graphically treated in order to present cleaner plots. I applied to the photoperiod, and the activity series an arithmetic moving average of period n = 7 in order to smooth out the original spiky curves.

Sample versus individual activity and migration patterns

I studied the activity and migratory patterns of Cory's Shearwater at the sample level (considering all 20 individuals in the sample). I also checked patterns at the individual level (each individual separately) to verify if the sample pattern deviates heavily from them.

The central limit theorem states that, given certain conditions, the mean of a sufficiently large number of independent random variables, each with finite mean and variance, will be approximately normally distributed. Although sample size is small (n = 20), I assumed that variables would tend to be normally distributed, including phenology variables as in figure 6.

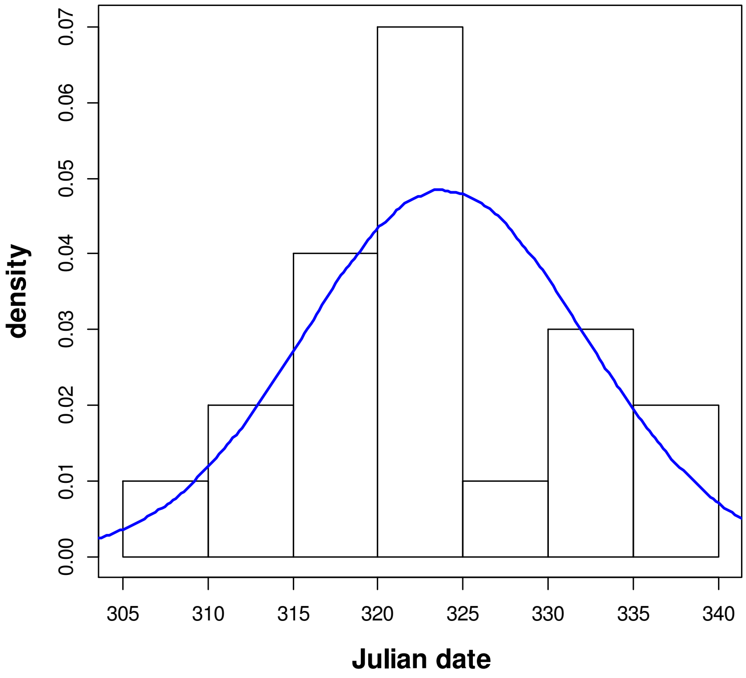

Figure 6. Empirical distribution of the date of initiation of the post-nuptial migration in the sample. The blue line is the pdf of a normal distribution with $\mu = \bar{x}$ and $\sigma = s$.

Following this assumption, I have used the mean in plots and analyses as an appropriate descriptor of the sample.

Missing values

I omitted from analyses the cases with missing values.

Factors influencing activity

Atmospheric and sea conditions may have a strong effect on the activity of Cory's Shearwater at small time scales: head winds or rain may force individuals to detour or to stop along their migratory journeys; overcast skies may reduce visibility, especially at night, making flight and food search difficult; rough seas may have similar effects on foraging. Despite their more than likely influence on the birds' activity, I disregarded implementing them in this study because Mk 4 geolocators only provide two positions per day and their positional error is large (185 ± 115 km), while Cory's Shearwaters can fly 1.000 km in one single day's run. To illustrate this let's imagine that the center of a storm of 200 km of radius is placed right on the midnight location fix exactly at the fixation time; taking into account the maximum error of 300 km, the storm could actually be 100 km away from the real position of the bird, and therefore have no influence on its activity. On the other hand, a storm can fully intercept a full moonlit leaving the bird in a pitch-dark night, hence reducing the real night-Moon overlap.

Here, I largely focused on the influence of Moon and photoperiod, which seemingly are the main factors that shape the activity patterns at a large scale. However, I also explored the influence of other predictors in the models, namely, annual phase and geographic position.

I have built multiple regression models to assess the factors that may influence flight activity (assumed to be normally distributed), and Poisson regression for the landing activity (a counting variable). I avoided building models with many factors and multiple interactions. I selected the multiple regression model which maximizes the adjusted R^2, and the Poisson regression model with minimum AIC.

I explored nocturnal activity because of two reasons: to ascertain the factors that influence nocturnal migration and to ascertain if the landing activity is influenced by lunar phase too, as is been shown in other shearwaters (Yamamoto et al 2008).

The annual phase is a categorical variable that I introduced in the models as four dummy variables (breeding, pre-nuptial migration, post-nuptial migration, winter).

I built three groups of models: 1) for the whole time series, 2) for the post-nuptial migration period, and 3) for the pre-nuptial migration period.

Periodicity

I analyzed autoregressive–moving-average ARMA (*p, q*) models using the residuals of the three best multiple regression models for the nocturnal flight activity: for the whole time series and the two migration periods. I built the eight possible models using low *p* autoregressive and *q* moving-average terms, concretely I gave them values = {0, 1, 2}.

To select the best model I used the Box-Jenkins methodology (Box and Jenkins 1970). First, I checked for stationarity; next, I dismissed lags beyond 10% of the sample size used (the first three lags for the migration periods). Then, I selected the model with lower AIC and with significant coefficients whose absolute values were larger than the standard errors. Finally, I built the autocorrelation function and the partial autocorrelation function diagrams from the residuals of these ARMA (1, 1) models in order to verify if there remained significant coefficients.

ARMA models are useful to reveal the correlational structure in a time series.

Spectral analysis provides an approach to identify the dominant and harmonic frequencies in a time series. I implemented this analysis to complement regression models and to reveal, if present, periodicities that can be directly linked to environmental cues. Thus, a dominant frequency= 0.034 would show a lunar month period (period= 1/freq), because the dataset contains daily data. To make a straightforward interpretation of the raw periodogram, I transformed the frequency of abscises into period.

Factors influencing migration

I provide graphical evidence of the correlation between migratory phenology and some factors that may have influence over the former.

A hatched vertical line on figures 8 to 12 indicates the opening date of the wind gates across the Intertropical Convergence Zone in 2002 (Felicísimo et al 2008). This line clearly shows that the end of the African summer monsoon sets the earliest likely date of the post-nuptial migration.

I have generated contour plots with plot.surface() of package fields based on models built from thin plate spline regression and using nocturnal flight activity as dependent variable and overlap + phase as independent variables.

I also fitted smooth spline regression lines to scatterplots of nocturnal activity versus latitude. A smoothing spline is a locally weighted average of the y's based on the relative locations of the x values and is an appropriate approach to reveal non-linear relations between variables. I generated these lines along with their standard errors applying function sreg() of package fields. This function fits a cubic spline to bivariate data using least-squares.

RESULTS AND DISCUSSION

Circadian patterns

Cory's Shearwater is largely a diurnal species as revealed by the activity record of loggers (figure 7). Its flight activity shows a bimodal daily pattern which peaks at crepuscular hours, whereas its landing activity shows a plateau during day time.

Circannual patterns

Total daily activity shows a moderate pattern throughout the year (figure 8):

- Flight activity is highest in August, drops to its minimum in early November, suddenly peaks in late November, drops back to the minimum during the whole winter, rises back from mid February until reaching its maximum in April, and descends slowly until June from which it bounces back over.
- Landing activity is more irregular and is not as complementary to flight activity as one would expect: peaks several times during the incubation period, drops to the annual minimum from then until the onset of the post-nuptial migration, plateaus during the whole winter season and drops back again with the onset of the pre-nuptial migration.

Visual comparison between nocturnal and diurnal corrected flight activities shows that diurnal ones are always greater. Interestingly, both activities are moderately to highly parallel (figure 9). When overlapping the photoperiod, we can also confirm a high parallelism: the absolute values of the slopes (obtained from a simple linear regression of the standardized values) are similar. The steep increase in slope of the photoperiod as the annual phases change is a consequence of the birds' migrations, not its cause (although migration could be triggered from a certain photoperiodic threshold, with the actual onset date fine-tuned by means of other environmental cues).

Corrected landing activity shows a more complex pattern (figure 10), with diurnal landings moderately to strongly correlated to photoperiod (especially during the non-breeding season) and overall nocturnal landings poorly correlated. The linear correlation coefficients for the whole interval are:

$r_{nocturnal} = -0.093$, $p < 0.001$; $r_{diurnal} = 0.380$, $p < 0.001$

Diurnal activity is apparently greater than nocturnal activity when we take the whole dataset. Both parametric and non-parametric tests assume that data are not correlated, therefore, the usual paired tests (Wilcoxon or t-test) cannot be used. A way around this problem is analyzing the time series of the difference between values of the original series (not done).

These differences in the daily activity routine raise a logical question: Are night time and day time patterns different? There are especially striking differences between them in the landing activity (figure 10).

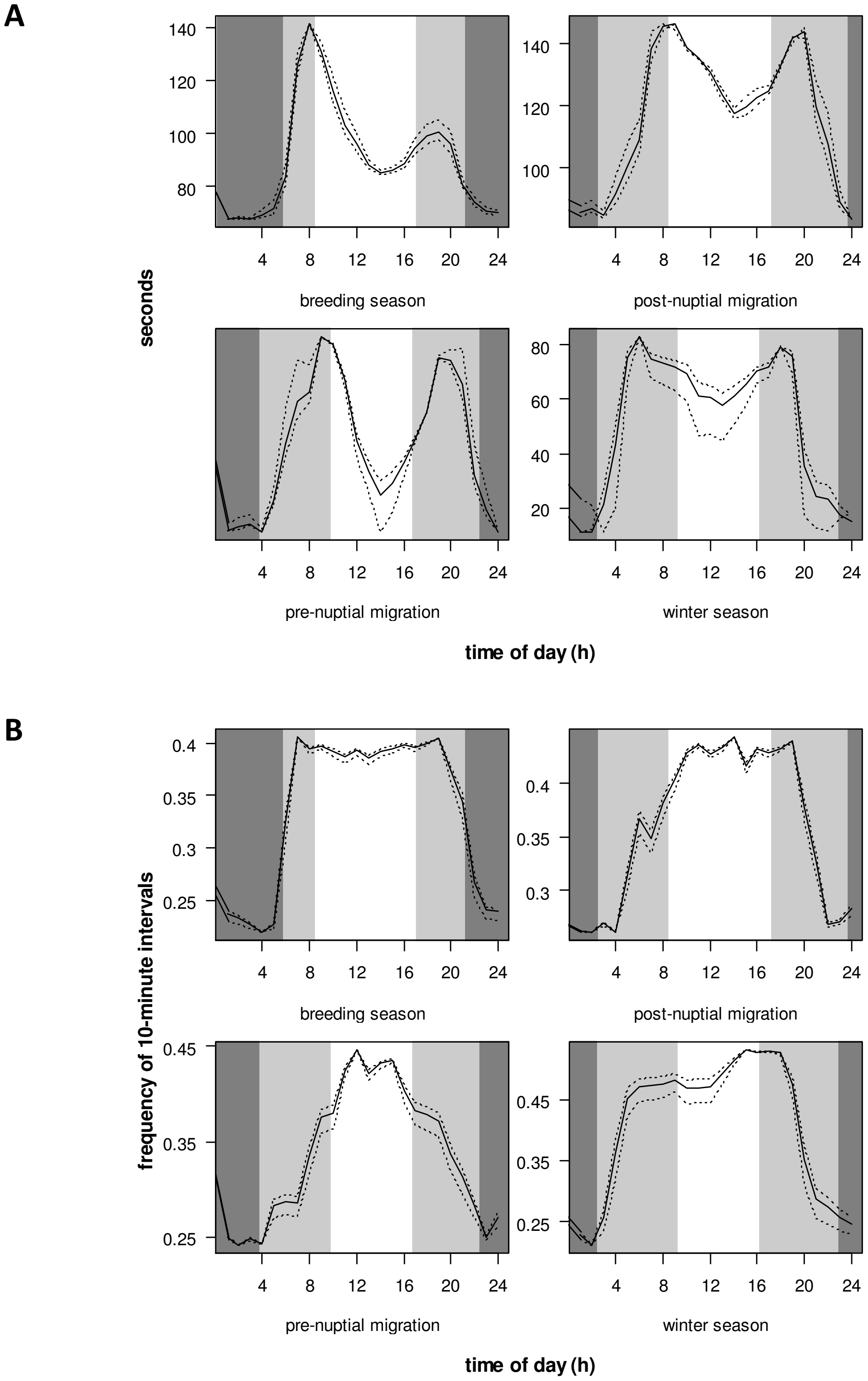

Figure 7. A) Hourly flight activity pattern for each annual phase. B) Hourly landing activity pattern for each annual phase.

Values of total activity have been averaged over the whole sample. Dark gray rectangles indicate night time over the whole period, light gray rectangles night time that only happens partially during the whole period, white rectangles indicate day time. Lines show mean ± SD, (continuous and hatched, respectively).

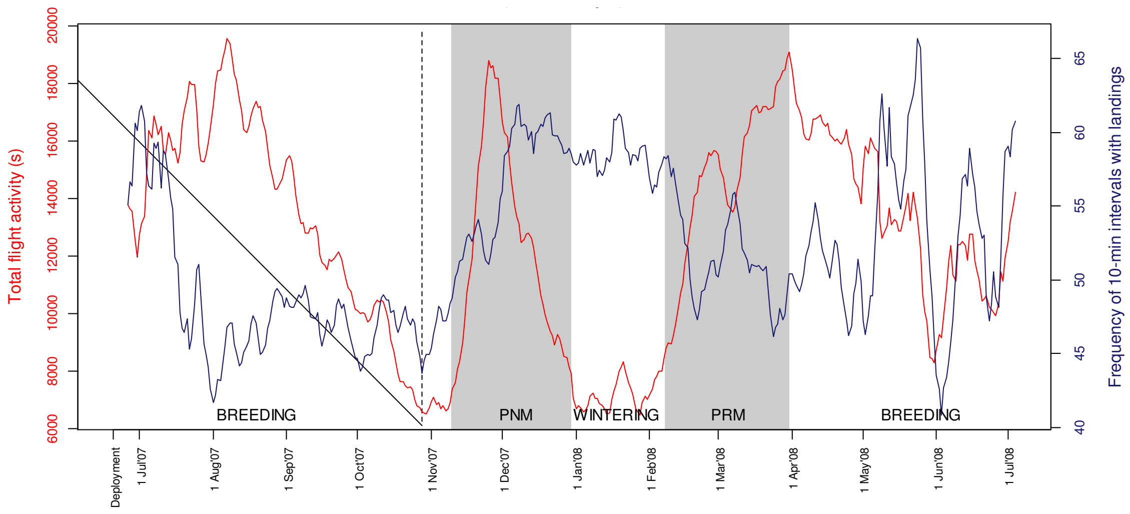

Figure 8. Total daily flight versus landing activity. Grey rectangles show the two migration periods. The hatched vertical line indicates the end of the summer African monsoon (which starts in early June) after which the prevailing westerly winds drop to a minimum. Annual phases are abridged in capital at the bottom.

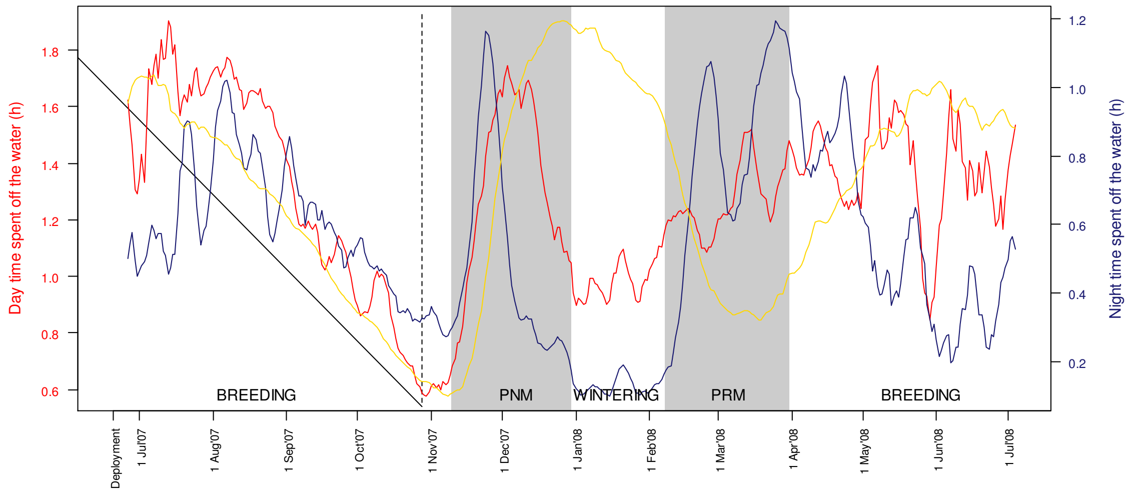

Figure 9. Nocturnal versus diurnal corrected flight activity. The gold line shows the evolution of photoperiod throughout the year at the mean local position (range = 11.69 - 14.72 h). Notice that direct comparison is not possible because of the different scales. Caption of figure 8 provides an explanation of the remaining elements.

The next logical question that rises is: Does the Moon exert an influence on the nocturnal activity? It does. Figure 11 shows a strong influence of Moon phase on the nocturnal flight activity in the post-nuptial migration. Surprisingly, Moon phase also seems to exert an influence on diurnal activity, as it suggests the overlap between several peaks. Figure 12 also shows a strong influence of Moon phase on the nocturnal landing activity in the pre-nuptial migration, and perhaps throughout the year, although with a certain lag. Diurnal landing activity seems much less influenced although there is a hint of peak overlaps between April and June.

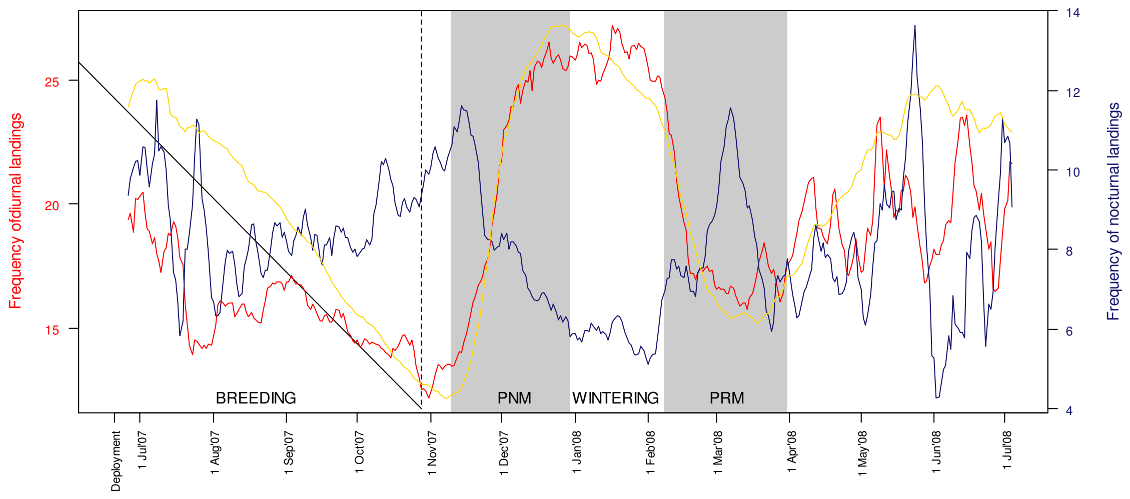

Figure 10. Nocturnal versus diurnal corrected landing activity. The gold line shows the evolution of photoperiod throughout the year at the mean local position of the birds (range = 11.69 - 14.72 h). Notice that direct comparison is not possible because of the different scales. Caption of figure 8 provides an explanation of the remaining elements.

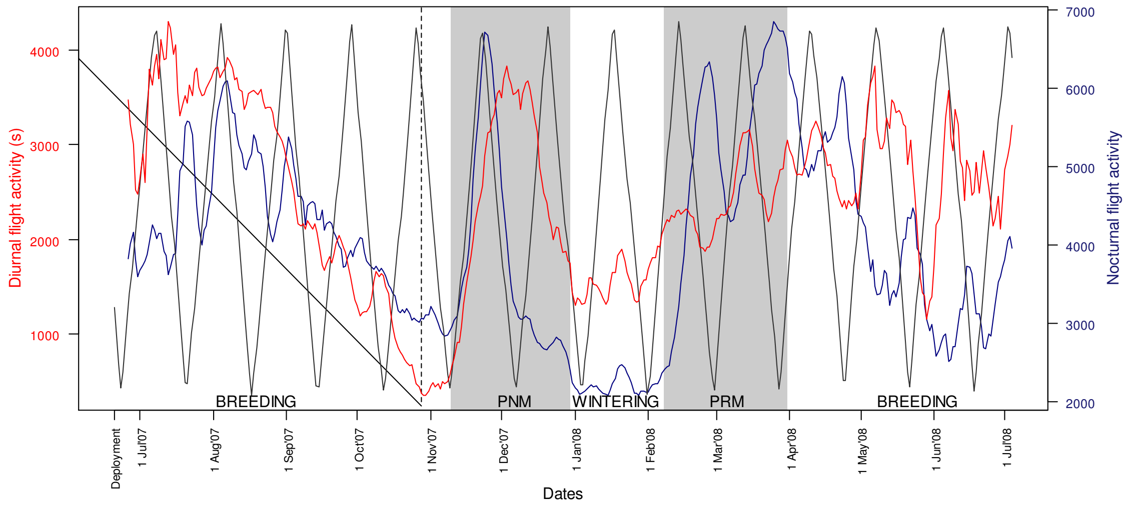

Figure 11. Diurnal and nocturnal corrected flight activity in relation to Moon phase. Caption of figure 8 provides an explanation of the remaining elements.

Activity patterns within the annual cycle

Cory's Shearwater reduces its activity as day-length grows shorter, coinciding with the onset of brooding. Its flight activity peaks with migration, as expected. Winter is a phase in which Cory's Shearwater engages principally in foraging, probably because of both a lack of competing tasks and a need to rebuild physical condition after the strenuous breeding efforts. Overall, Cory's Shearwater avoids photoperiods with longer night than day: it lives in a perpetual summer, as other shearwaters do (Shaffer et al 2006), probably to exploit oceans resources at their production peak.

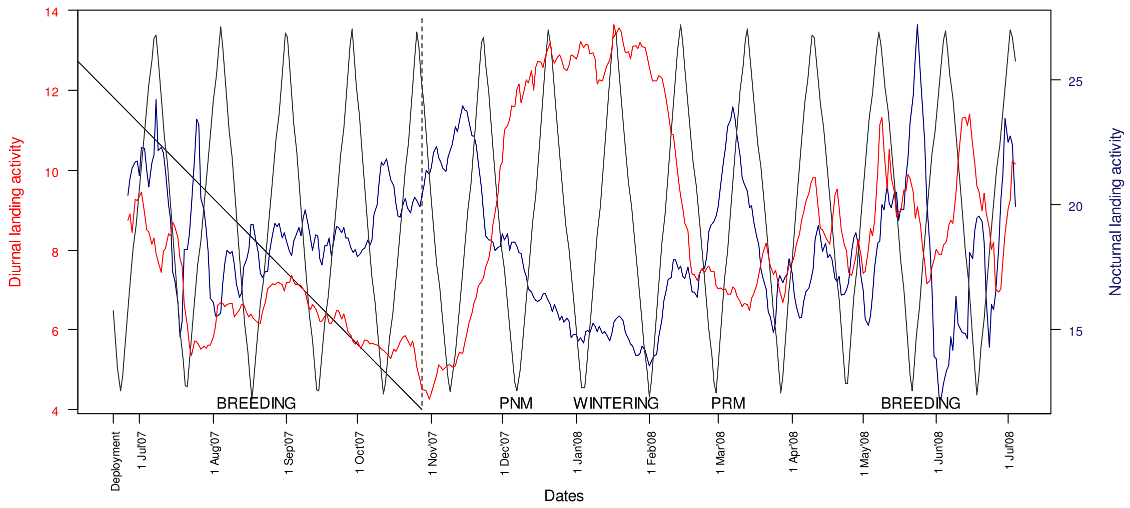

Figure 12. Diurnal and nocturnal corrected landing activity in relation to Moon phase. Caption of figure 8 provides an explanation of the remaining elements.

Factors influencing activity

The multiple regression models that best fit the whole time series using the nocturnal flight activity as response variable are the ones that include annual phase as predictor (table 2).

Model	significant predictors	R^2 adj (%)
whole time series		
phase + photoperiod + latitude + longitude	all	15.8
phase * photoperiod + latitude + longitude	all	16.1
phase * photoperiod	all	6.1
phase + photoperiod	all	5.9
AP	all	20.7
AP + phase*photoperiod	all	23.9
AP + phase + photoperiod	all	23.5
AP + phase + photoperiod + latitude + longitude	all	24.0
latitude + longitude	all	12.7
overlap + phase + photoperiod	pha, pho	6.0
post-nuptial migration		
overlap + phase	all	25.4
phase + photoperiod	all	31.6
overlap + phase + photoperiod	all	38.2
pre-nuptial migration		
overlap + phase	all	39.2
phase + photoperiod	all	37.9
overlap + phase + photoperiod	all	40.3

Table 2. Summary of the multiple regression models fitted to the whole time series and the two migration periods using the nocturnal flight activity as response variable. Shading indicates selected model. AP= annual phase (actually 4 dummy variables).

Poisson regression models that use nocturnal landing activity as response variable also point lunar phase as an important factor that shapes this activity (table 3). The models that best fit the whole time series are the ones that include lunar phase, annual phase and position as predictors. Phase and photoperiod are the best predictors for the migration periods.

model	significant predictors	AIC
whole time series		
phase + photoperiod + latitude + longitude	pha, lat, long	45,052
phase * photoperiod + latitude + longitude	lat, long	45,046
phase * photoperiod	all	45,225
phase + photoperiod	all	45,234
AP	winter	45,171
AP + phase*photoperiod	pho, winter	45,080
AP + phase + photoperiod	pha, winter	45,084
AP + phase + latitude + longitude	pha, lat, long, winter	45,037
latitude + longitude	all	45,112
latitude + longitude + phase	all	45,055
post-nuptial migration		
overlap + phase	all	4,384.1
phase + photoperiod	all	4,315.1
overlap + phase + photoperiod	all	4,280.9
pre-nuptial migration		
overlap + phase	all	2,893.9
phase + photoperiod	all	3,061.7
overlap + phase + photoperiod	all	2,879.2

Table 3. Summary of the Poisson regression models fitted to the whole time series and the migration periods using nocturnal landing activity as response variable. Shading indicates selected model. AP= annual phase.

The Moon has a strong influence on the nocturnal flight activity, especially during the migration period. Reasons behind this remain unexplored. The Moon does not seem to be useful as a navigation compass. On the other hand, intense moonlight may increase the efficiency of flight in birds that glide near the sea surface by increasing the input of visual information.

Yamamoto et al (2008) showed the lunar influence on the landing activity of a congeneric, the Streaked Shearwater *Calonectris leucomelas*. My conservative approach to the estimation of the frequency of landings could explain the relatively weak influence of the lunar phase on this variable. According to Phalan et al (2007) there is a very high correlation (r= 0.94) between the number of wet bouts and the number of landings in albatrosses. Although this relation could differ in shearwaters, future analyses should implement this approach.

Output of the best models is included in the annexes.

Periodicity

ARMA (1, 1) models are the ones that best fit the activity data (table 4). The whole time series is not stationary, as shown by the autocorrelation function (figure 13), and needs other techniques to be analyzed.

series	AR (SE)	MA (SE)	intercept (SE)	σ^2	AIC
whole series	0.993 (0.002)	-0.944 (0.006)	0.514 (415.2)	1.07e8	83,830
post-nuptial	0.566 (0.077)	-0.159 (0.090)	-8.016 (255.3)	7.95e7	8,529
pre-nuptial	0.997 (0.001)	-0.944 (0.005)	4,276.9 (850.5)	1.16e8	5,402

Table 4. Output of the best ARMA (1, 1) models. SE= standard error.

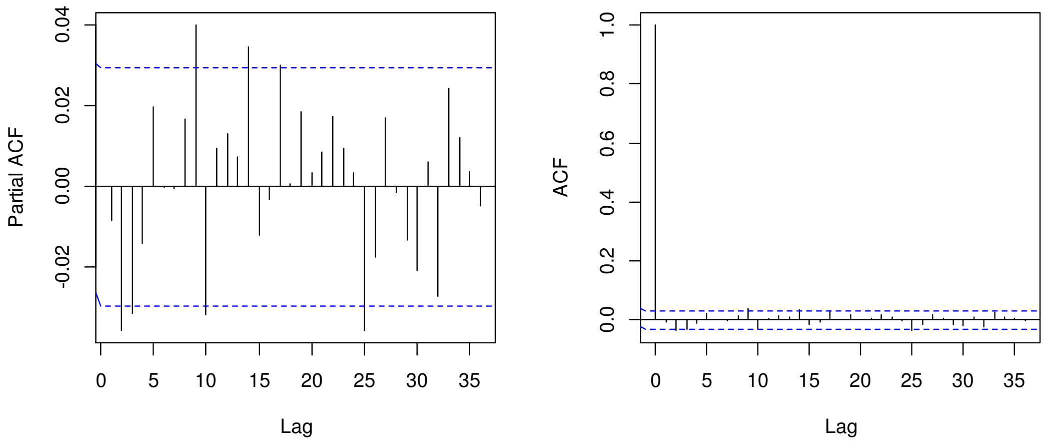

Figure 13. Autocorrelation function and partial ACF for the whole time series based on the residuals of the best ARMA model based on its stead on the best multiple regression model obtained for the nocturnal flight activity.

Time series for the nocturnal flight activity during the migration periods seem to be stationary and lack seasonality. Nocturnal flight activity during the migratory period has a significant coefficient of autocorrelation of order 1, and therefore the flight activity of one night is only correlated to the one of the previous night (figure 14).

The estimated coefficients of the ARMA models, however, are very close to 1 suggesting that ARMA models do not adjust well. To overcome this problem, I fitted a differential filter of order 1 to the ARMA(1, 1) models for the migration periods. Now, the autoregressive coefficients are significant but not as close to 1 but moving-average coefficients still are (table 5, figure 15). These results suggest that the analysis of these series still needs further work to be properly addressed.

series	AR (SE)	MA (SE)	σ^2	AIC
post-nuptial	0.369 (0.077)	-1.000 (0.014)	9.75e7	5,387
pre-nuptial	0.435 (0.043)	-0.994 (0.085)	8.04e7	8,517

Table 5. Output of the ARIMA (1, 1, 1) models. SE= standard error.

Circadian periods are easily revealed in the spectral density plots (figure 16). The 24 h signal is very prominent, although there is a strong signal for a period of 12 h especially for the flight activity that could be associated with the night/day transition or an internal clock.

Circannual patterns are less evident and the separate analyses of nocturnal and diurnal flight and landing activities yield some strange periods. The most important periods are all divisors of 384, which is 13 times the length of a synodic lunar month (29.54 days). All periodograms obtained for the different types of activity considered show 384 and 128 among their three most important harmonics (table 6).

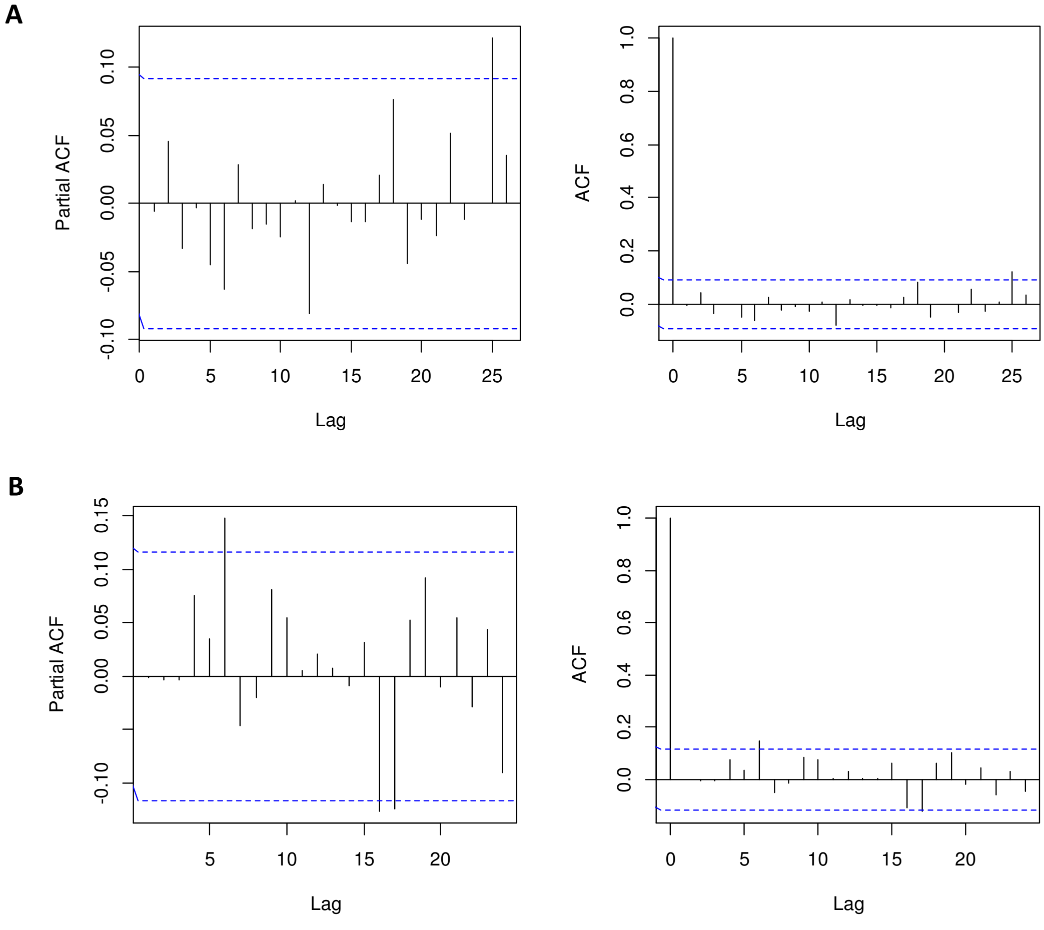

Figure 14. Autocorrelation function and partial ACF for the segment of the time series that comprises A) the post-nuptial migration, and B) the pre-nuptial migration, based on the residuals of the best ARMA model based on its stead on the best multiple regression model obtained for the nocturnal flight activity.

These results are really striking, since instead of revealing periods that are harmonics of the solar year show divisors of the “lunar year”, which is the multiple of lunar months closest to one solar year: 13. Thus, 192, 128, 96, 76, 64, 54.8, 29.54 and 16 divide the “lunar year” by 2, 3, 4, 5, 6, 7, 13 and 24, respectively. A lunar month periodicity is only apparent in the periodogram of the nocturnal flight activity (figure 17).

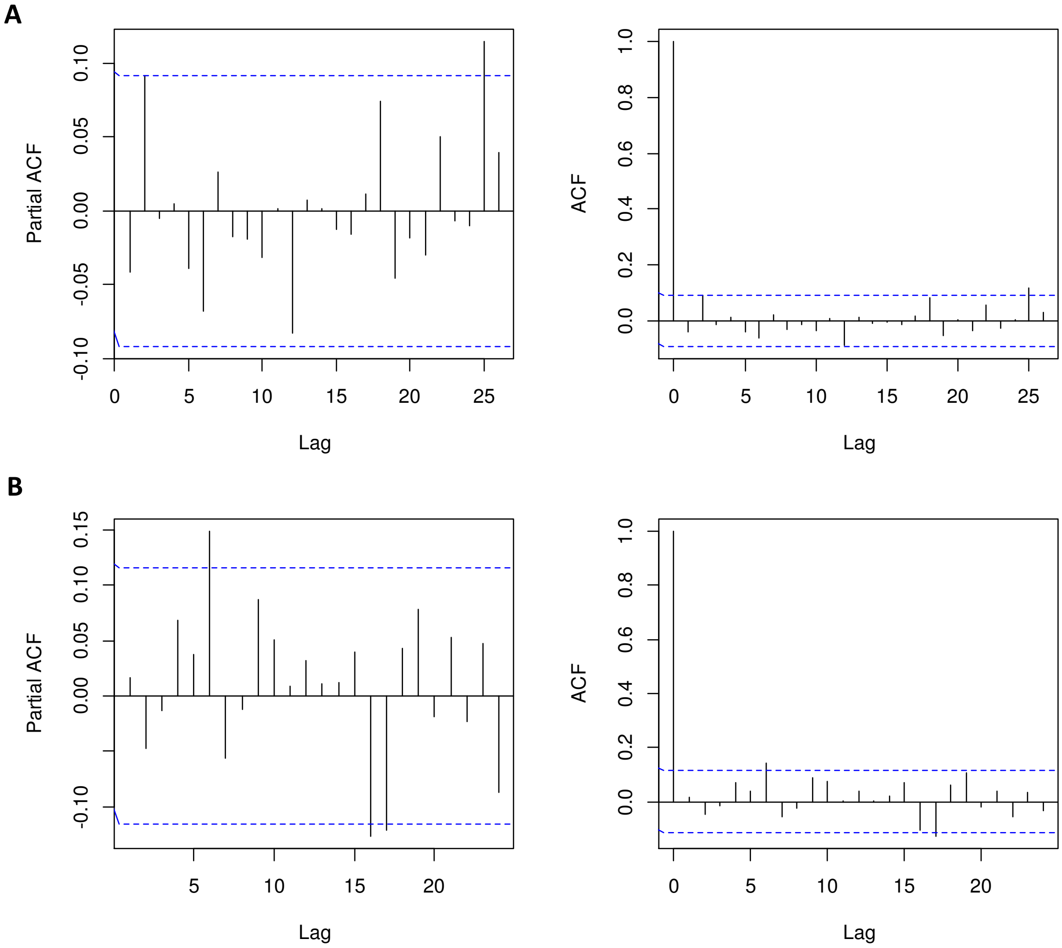

Figure 15. Partial ACF and ACF for the ARIMA (1, 1, 1) models based on the best ARMA (1, 1) models previously obtained. A) Post-nuptial migration; B) Pre-nuptial migration.

periodogram	**periods**
nocturnal flight activity	192, 128, 384, 76, 29.54
diurnal flight activity	128, 384, 96, 192, 54.8
nocturnal landing activity	384, 192, 128, 96
diurnal landing activity	384, 128, 96, 16, 64

Table 6. Most important periods in descendant order for the daily activity periodograms.

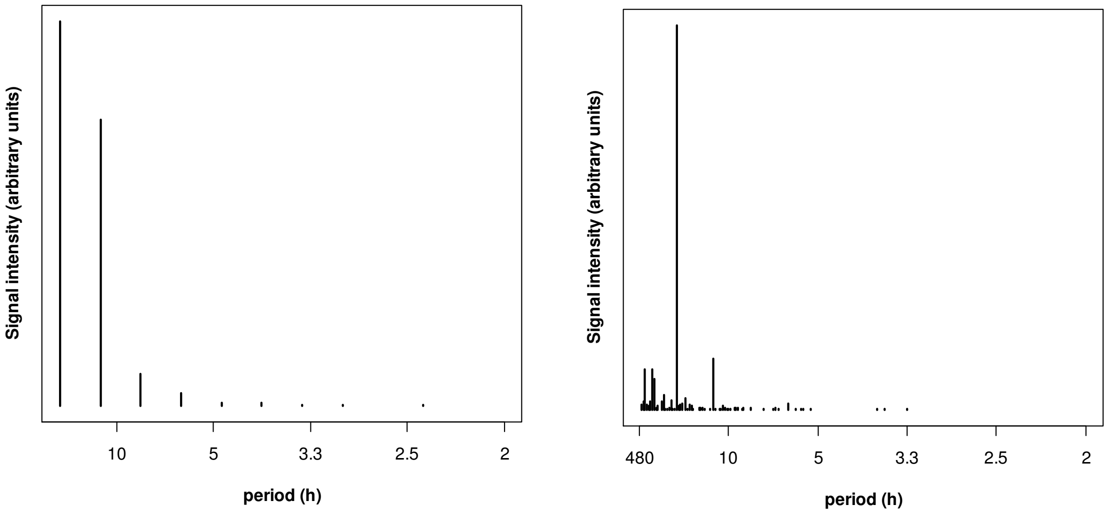

Figure 16. Periodograms of hourly flight activity (left) and hourly landing activity (right). The two most prominent spikes correspond to the 24.00 and 12.00 h harmonics, respectively.

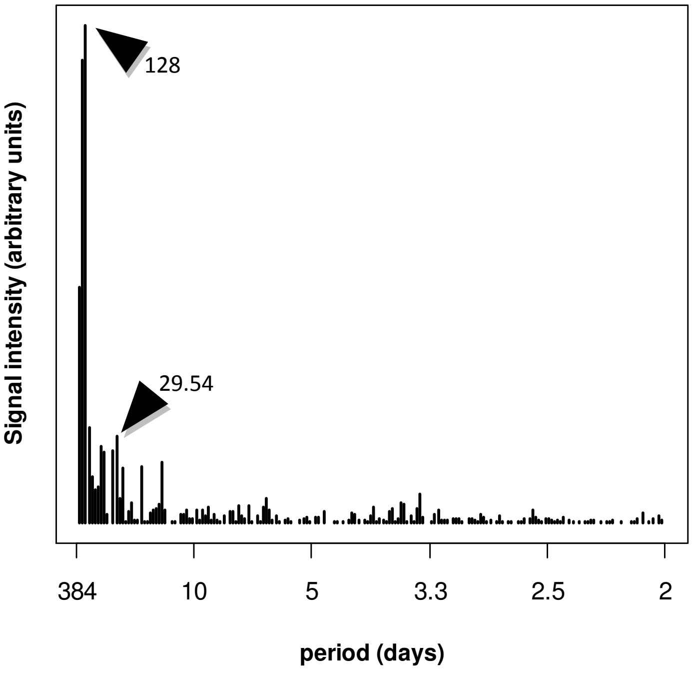

Figure 17. Periodogram of nocturnal flight activity for the whole interval of study. The five most prominent spikes in descendent order are: 128, 192, 384, 96 and 29.54 days.

Factors influencing migration

Onset of migration may depend on multiple factors, such as lunar phase, photoperiod, location of the winter area or sex. Protandry, the earlier arrival of males at the breeding grounds is a pervasive phenomenon in bird migration (Alerstam 1982). The 10 males in the sample arrive in the breeding grounds nine days earlier than the 10 females (median values, see table 7). Differences are non-significant however (Wilcoxon test: W = 31, p = 0.16), but this lack of significance can be an artifact produced by low sample size.

A mild protoginy, the earlier migration of females, happens in some species (Mills 2005). Males in the sample start the post-nuptial migration five days earlier than females (median values). Again, this difference is not significant (Wilcoxon test: W = 26.5, p = 0.08).

Analogous comparisons of the onset of the pre-nuptial migration and of the arrival at winter areas yield similar results (p> 0.05), although closer to significance ought to the dispersion of the values.

sex	**onset of post-nuptial migration**	**arrival at winter areas**	**onset of pre-nuptial migration**	**arrival at breeding areas**
males (10)	16/11/07 ± 10d	06/12/07 ± 7d	19/02/08 ± 12d	07/03/08 ± 14d
females (10)	21/11/07 ± 8d	10/12/07 ± 16d	18/02/08 ± 5d	16/03/08 ± 19d
sample (20)	19/11/07 ± 9d	06/12/07 ± 6d	19/02/08 ± 9d	15/03/08 ± 16d
r	0.25	0.52	0.37	-0.30

Table 7. Median ± median absolute (days) deviation dates for the onset of each annual phase by sex (sample size within parenthesis). Bottom row: coefficients of correlation between each date and lunar phase (all p < 0.05).

Duration of pre-nuptial migration is believed to be shorter than post-nuptial migration (Bauchinger and Klaassen 2005). The mean ± SD obtained for the sample indicates that this is also the case for Cory's Shearwater (21.20 ± 7.35 and 24.00 ± 8.28, respectively), although differences are non-significant again (Wilcoxon pair test: V = 73, p-value = 0.24).

The effect of likely predictors of onset and arrival of migration, such as lunar phase, photoperiod, sex, colony of origin and geographic position could be tested using generalized linear models. Unfortunately, the sample size is way too small to build reliable model: there are only 10 males and 10 females. Nevertheless, correlation coefficients suggest a moderate influence of the Moon phase on the onset of each annual phase (table 7).

A hidden factor on the Moon influence is night-Moon overlap. If moonlight helps increasing the efficiency of nocturnal flight, then it seems logic that the more hours of moonlight in the night the better for the flying bird. During the post-nuptial migration the flight activity of Cory's Shearwater increases as both night-Moon overlap and lunar phase increase; however, flight activity increases with lunar phase but is nearly independent of night-Moon overlap during the pre-nuptial one (figure 18). Day-length grows longer (*i.e.* night-length grows shorter) during the post-nuptial migration (see figures 9 and 10), pushing the birds to increase their activity in nights with large night-Moon overlap, especially as the Moon waxes. Day-length is approximately constant during the pre-nuptial migration, and therefore birds only increase their effort with waxing Moon.

When we think of the factors that may influence migration phenology we have in mind invariant states (such as sex), and present or recently happened conditions. However, conditions lying ahead in time and/or space may have an even stronger influence.

In figures 8 to 12, I marked with a vertical hatched line the end of the African summer monsoon. During the monsoon, prevailing near-surface winds in the central Atlantic show a dominant westerly component, and form a low pressure belt from French Guiana to the Mauritania-Senegal coast at the so called Intertropical Convergence Zone (Felicísimo et al 2008). This belt constitutes an aerial barrier because it would increase the energy required to Cory's Shearwater in order to cross it. All the birds in the sample, as well as those included in the study by Felicísimo et al (2008) started the postnuptial migration after the end of the African summer monsoon.

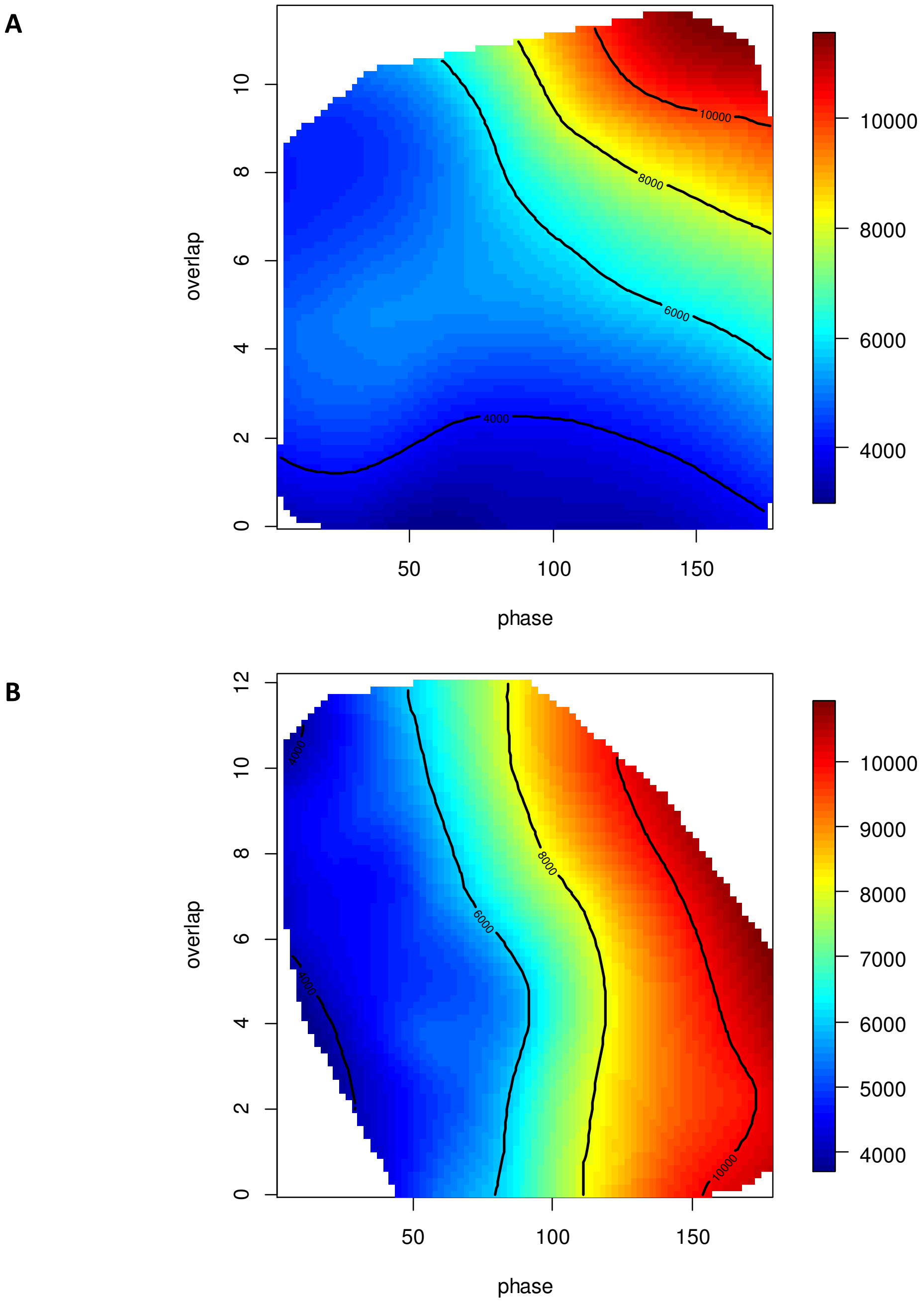

Figure 18. Contour plots showing the relationship of nocturnal flight activity with night-Moon overlap and with lunar phase in A) the postnuptial migration and B) the pre-nuptial migration. The plot has been built from the best multiple regression models and fixing phase and overlap.

On the other hand, spring arrivals may be predicted by the North Atlantic Oscillation, as showed Vähätalo et al (2004). As far as I know, this influence remains unexplored in seabirds.

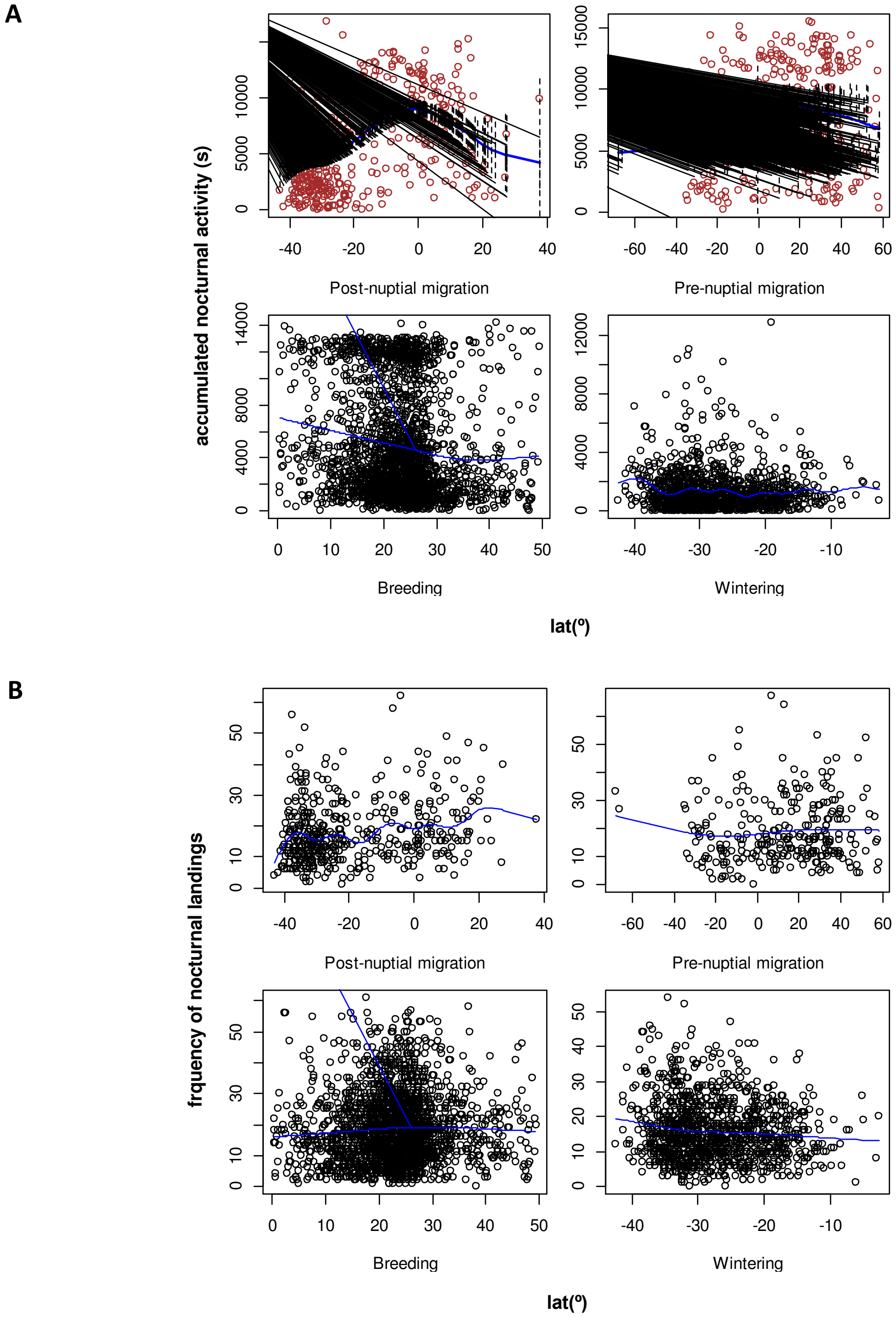

Figure 19. Spline lines (blue) fitted to the scatterplot of latitude versus A) accumulated nocturnal flight activity, and B) frequency of nocturnal landings. The top two plots show the standard error of the spline lines (hatched vertical segments).

As implied by Felicísimo et al (2008), the equatorial zone is a geographic barrier that migratory seabirds, including Cory’s Shearwaters, would try to leave behind as soon as possible. Smooth-spline lines fitted to the relationship between latitude and activity indicate that the latter increases around the equator, suggesting that the Intertropical Convergence Zone is a geographic barrier to migration, especially during the post-nuptial journey (figure 19).

The latitude at which the maximum nocturnal flight activity is reached lies below the equator in the post-nuptial migration and above it in the pre-nuptial migration (figure 20).

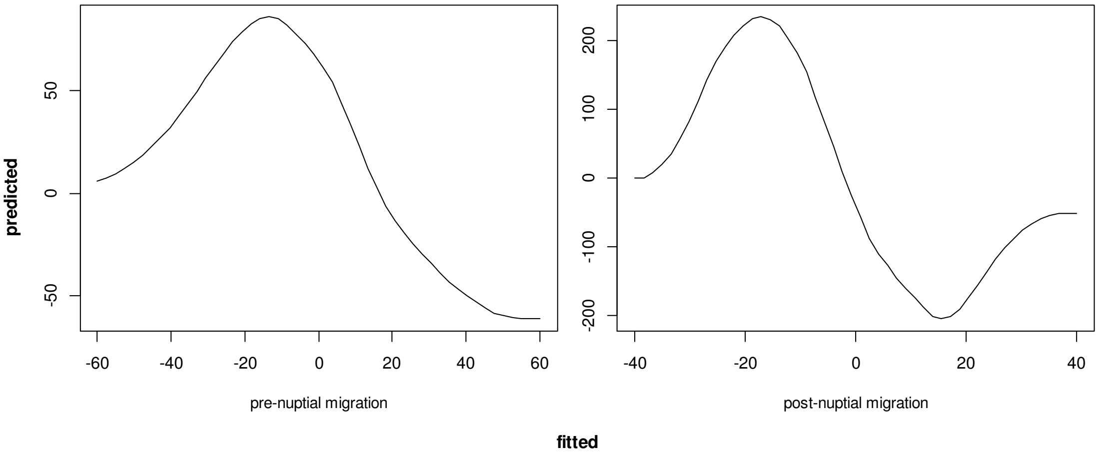

Figure 20. Derivatives of the spline fitted values for the migration periods.

CONCLUSION

The activity of Cory's Shearwater is primarily shaped by the annual phase, but also by photoperiod and lunar phase, with the geographic location also playing an important role when considering the whole time series. The latter is not surprising as this species basically forages in specific oceanic areas (Navarro et al 2008). The lunar influence on the nocturnal flight activity is especially strong during the migration periods, particularly at the individual level (some birds have r> 0.8). The species' annual activity pattern shows striking parallelisms between photoperiod and flight activity especially from the end of the incubation period until the onset of the winter period, and between photoperiod and diurnal landing activity from the onset of the postnuptial migration until the onset of the breeding period.

One of the most interesting results of this work comes from the analysis of periodicity, since Cory's Shearwater seemingly follows circadian rhythms at a small time scale but lunar rhythms at larger scales, concretely a circannual rhythm linked to the "lunar calendar" (13 synodic lunar months).

Migration is the period of flight activity par excellence; however, factors that determine its phenology are not obvious. For example, most migratory passerines molt before leaving their breeding grounds (Jenni and Winkler 1994), but large birds cannot squeeze a complete molt episode between breeding and migration (Rohwer et al 2009). Cory's Shearwater is not an exception (Ramos et al 2009). Large non passerine birds also have a very protracted reproductive period, which in Cory's Shearwater lasts until September or early October (Reyes-González and González-Solís 2012). However, even individuals that failed to breed successfully during the season delayed their migration until October. The most likely factor that has fixed a time threshold for the initiation of the post-nuptial migration is the African summer monsoon. Cory's Shearwater is a gliding seabird that uses surface winds for an optimal flying (González-Solís et al 2009), and avoids the blocking winds that would meet before the end of the monsoon. Since the end of the monsoon could vary between years, birds may leave a "security margin" to avoid getting trapped. Precisely, flight activity peaks while birds cross these latitudes, suggesting that this is an aerial barrier.

Males and females tend to differ in their migration timing, with males tending to leave and arrive earlier. Proper analyses to reveal this and other likely factors that may influence migration timing await a larger sample size, however. Small sample size has also precluded reliable testing of the duration of the migratory journey, although differences between them go in the expected direction, with shorter pre-nuptial compared to post-nuptial durations.

Future research

Geolocators have widened the scope of the study of seabirds: migratory routes, winter areas, foraging behavior, exposure to commercial fishing lines, among many others (Burger and Shaffer 2008) have been ascertained. Further sophistication and miniaturization of bio-loggers in general will allow going still much farther; by increasing battery duration, memory capacity and data resolution and type ornithologists will increase their knowledge on the biology of seabirds while minimizing disturbance to the individuals. Indeed, new geolocator models record the activity at a finer time resolution, which will result in a more realistic estimation of the landing activity.

The relevance of this work has been reduced by the small sample size. Future research will obviously have to overcome this limitation.

Inaccuracy of annual phase dates has been another limitation of this work. Activity could be used to estimate the onset of migration. Onset of migration is accompanied by a sudden change of flight activity (figure 8, 9 and 11). Before application, it should be ascertained, however, if there is a previous increase in “void” activity or Zugunruhe, and for how long it anticipates migration on average. This can only be achieved if geographic position is sufficiently precise.

Another improvement associated to precise data on geographic position is the implementation of weather data into the analyses. The combination of real-time and real-position environmental data will allow small time scale analyses and their influence on behavior.

This work is a contribution to the still incipient study field of seabird activity, and many ecological questions related to this topic can be still addressed using the current geolocators: migration stopovers, prey-seabird correlations, carry over effects of migration on breeding success, comparison between colonies and years, variation in activity between individuals, learning process in immature birds, synchronization of processes such as egg laying, colony arrival and prelaying period.

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ANNEXES

MULTIPLE REGRESSION MODELS

1) Whole series

```
lm(formula = actn ~ fen + phase + photoperiod + lat + long, data = final)

Residuals:
   Min      1Q  Median      3Q     Max
-7329.3 -2703.9  -763.9  1612.0 12199.1

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -3363.874   1031.884  -3.260  0.00112 **
fenmpn       565.518    241.314   2.343  0.01915 *
fenmpr      2823.701    229.396  12.309  < 2e-16 ***
fenwin     -3270.786    244.512 -13.377  < 2e-16 ***
phase         11.761      1.069  10.998  < 2e-16 ***
photoperiod   526.506     77.242   6.816 1.06e-11 ***
lat           10.569      4.152   2.545  0.01095 *
long          19.481      4.375   4.453 8.68e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 3594 on 4396 degrees of freedom
Multiple R-squared: 0.2409,     Adjusted R-squared: 0.2397
F-statistic: 199.3 on 7 and 4396 DF,  p-value: < 2.2e-16
```

2) Post-nuptial migration

```
lm(formula = actn ~ overlap + phase + photoperiod, data = fmpn2)

Residuals:
   Min      1Q  Median      3Q     Max
-7995.2 -2129.3  -113.2  2035.8 10779.1

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) 20539.779   1936.711  10.605  < 2e-16 ***
overlap       357.601     51.076   7.001 9.24e-12 ***
phase          19.772      3.237   6.109 2.17e-09 ***
photoperiod -1321.302    135.996  -9.716  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 3159 on 451 degrees of freedom
```

```
Multiple R-squared: 0.386,	Adjusted R-squared: 0.3819
F-statistic: 94.49 on 3 and 451 DF,  p-value: < 2.2e-16
```

3) Pre-nuptial migration

```
lm(formula = actn ~ overlap + phase + photoperiod, data = fmpr2)

Residuals:
   Min     1Q  Median     3Q    Max
-9453.9 -2227.5  -179.6  1890.3  9678.8

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) 13256.455   4910.327    2.70 0.007361 **
overlap       214.637     62.036    3.46 0.000624 ***
phase          56.721      4.318   13.13  < 2e-16 ***
photoperiod  -944.746    387.201   -2.44 0.015308 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 3375 on 281 degrees of freedom
Multiple R-squared: 0.4091,	Adjusted R-squared: 0.4028
F-statistic: 64.84 on 3 and 281 DF,  p-value: < 2.2e-16
```

POISSON REGRESSION MODELS

1) Whole series

```
glm(formula = nmar ~ lat + long + phase, family = poisson, data = final)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-6.0640  -1.8896  -0.3904   1.2299   8.5589

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  2.888e+00  7.429e-03 388.696  < 2e-16 ***
lat          1.706e-03  1.588e-04  10.745  < 2e-16 ***
long         2.143e-03  2.459e-04   8.714  < 2e-16 ***
phase       -5.397e-04  7.041e-05  -7.666 1.78e-14 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 25535  on 4403  degrees of freedom
Residual deviance: 25075  on 4400  degrees of freedom
AIC: 45055
```

2) Post-nuptial migration

```
glm(formula = nmar ~ overlap + phase + photoperiod, family = poisson,
    data = fmpn2)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-4.8029  -1.6587  -0.5442   0.9330   7.7505

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  4.4829718  0.1401188  31.994  < 2e-16 ***
overlap     -0.0234024  0.0038925  -6.012 1.83e-09 ***
phase       -0.0007211  0.0002481  -2.906  0.00366 **
photoperiod -0.1028961  0.0100010 -10.289  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)
```

```
    Null deviance: 2362.1  on 454  degrees of freedom
Residual deviance: 2194.1  on 451  degrees of freedom
AIC: 4280.9
```

3) Pre-nuptial migration

```
glm(formula = nmar ~ overlap + phase + photoperiod, family = poisson,
    data = fmpr2)


Deviance Residuals:
    Min       1Q   Median       3Q      Max
-5.5287  -1.7838  -0.4188   1.1700   7.2770


Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  5.0266882  0.3465444  14.505  < 2e-16 ***
overlap     -0.0579118  0.0043338 -13.363  < 2e-16 ***
phase       -0.0047316  0.0002999 -15.776  < 2e-16 ***
photoperiod -0.1129703  0.0277404  -4.072 4.65e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


(Dispersion parameter for poisson family taken to be 1)


    Null deviance: 1897.7  on 284  degrees of freedom
Residual deviance: 1566.6  on 281  degrees of freedom
AIC: 2879.2
```