



Seabird Migration Strategies: Flight Budgets, Diel Activity Patterns, and Lunar Influence

Anne-Sophie Bonnet-Lebrun^{1,2*}, Maria P. Dias^{1,3}, Richard A. Phillips², José P. Granadeiro⁴, M. de L. Brooke⁵, Olivier Chastel⁶, Thomas A. Clay⁷, Annette L. Fayet⁸, Olivier Gilg^{9,10}, Jacob González-Solís¹¹, Tim Guilford⁸, Sveinn A. Hanssen¹², April Hedd¹³, Audrey Jaeger¹⁴, Johannes Krietsch^{15,16}, Johannes Lang^{10,17}, Matthieu Le Corre¹⁴, Teresa Militão¹¹, Børge Moe^{18,19}, William A. Montevecchi²⁰, Hans-Ulrich Peter¹⁵, Patrick Pinet^{14,21}, Matt J. Rayner^{22,23}, Tim Reid²⁴, José Manuel Reyes-González¹¹, Peter G. Ryan²⁵, Paul M. Sagar²⁶, Niels M. Schmidt^{27,28}, David R. Thompson²⁹, Rob van Bemmelen^{30,31}, Yutaka Watanuki³², Henri Weimerskirch⁶, Takashi Yamamoto³³ and Paulo Catry¹

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*Correspondence:

Anne-Sophie Bonnet-Lebrun
anne-sophie.bonnet-lebrun@normale.fr

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¹ MARE – Marine and Environmental Sciences Centre, ISPA - Instituto Universitário, Lisbon, Portugal, ² British Antarctic Survey, Natural Environment Research Council, Cambridge, United Kingdom, ³ BirdLife International, Cambridge, United Kingdom, ⁴ CESAM and Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal, ⁵ Department of Zoology, University of Cambridge, Cambridge, United Kingdom, ⁶ Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 CNRS - Université de la Rochelle, Villiers-en-Bois, France, ⁷ School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom, ⁸ Department of Zoology, University of Oxford, Oxford, United Kingdom, ⁹ UMR 6249 Chrono-environnement, Université de Bourgogne Franche-Comté, Besançon, France, ¹⁰ Groupe de Recherche en Ecologie Arctique, Francheville, France, ¹¹ Institut de Recerca de la Biodiversitat (IRBio) and Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Barcelona, Spain, ¹² Norwegian Institute for Nature Research (NINA), FRAM – High North Research Centre for Climate and the Environment, Tromsø, Norway, ¹³ Wildlife Research Division, Environment and Climate Change Canada, Mount Pearl, NL, Canada, ¹⁴ UMR ENTROPIE, Université de La Réunion, IRD, CNRS, IFREMER, Université de Nouvelle-Calédonie, Université de La Réunion, La Réunion, France, ¹⁵ Institute of Ecology and Evolution, Friedrich Schiller University, Jena, Germany, ¹⁶ Department of Behavioral Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Seewiesen, Germany, ¹⁷ Working Group Wildlife Research at the Clinic for Birds, Reptiles, Amphibians and Fish, Justus Liebig University Giessen, Giessen, Germany, ¹⁸ Norwegian Institute for Nature Research (NINA), Trondheim, Norway, ¹⁹ Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway, ²⁰ Psychology Department, Memorial University, St. John's, NL, Canada, ²¹ Terres Australes et Antarctiques Françaises, La Réunion, France, ²² Auckland Museum, Auckland, New Zealand, ²³ School of Biological Sciences, University of Auckland, Auckland, New Zealand, ²⁴ CSIRO Oceans and Atmosphere, Hobart, TAS, Australia, ²⁵ FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa, ²⁶ National Institute of Water and Atmospheric Research Ltd., Christchurch, New Zealand, ²⁷ Department of Bioscience, Aarhus University, Roskilde, Denmark, ²⁸ Arctic Research Centre, Aarhus University, Aarhus C, Denmark, ²⁹ National Institute of Water and Atmospheric Research Ltd., Wellington, New Zealand, ³⁰ Wageningen Marine Research, Wageningen University and Research, IJmuiden, Netherlands, ³¹ Bureau Waardenburg, Culemborg, Netherlands, ³² Graduate School of Fisheries Sciences, Hokkaido University, Hakodate, Japan, ³³ Organization for the Strategic Coordination of Research and Intellectual Properties, Meiji University, Tokyo, Japan

Every year, billions of birds undertake extensive migrations between breeding and non-breeding areas, facing challenges that require behavioural adjustments, particularly to flight timing and duration. Such adjustments in daily activity patterns and the influence of extrinsic factors (e.g., environmental conditions, moonlight) have received much more research attention in terrestrial than marine migrants. Taking advantage of the widespread deployment in recent decades of combined light-level geolocator-immersion loggers, we investigated diel organisation and influence of the moon on flight activities during the non-breeding season of 21 migrant seabird species from a wide taxonomic range (6 families, 3 orders). Migrant seabirds regularly stopped (to either feed or rest)

during migration, unlike some terrestrial and wetland birds which fly non-stop. We found an overall increase for most seabird species in time in flight and, for several species, also in flight bout duration, during migration compared to when resident at the non-breeding grounds. Additionally, several nocturnal species spent more of the day in flight during migration than at non-breeding areas, and vice versa for diurnal species. Nocturnal time in flight tended to increase during full moon, both during migration and at the non-breeding grounds, depending on species. Our study provides an extensive overview of activity patterns of migrant seabirds, paving the way for further research on the underlying mechanisms and drivers.

Keywords: bird migration, ecological barriers, nocturnality, migratory behaviour, moon phases, transequatorial migrants

INTRODUCTION

Every year, billions of birds migrate between breeding and non-breeding areas, often undertaking extensive journeys across unfavourable environments. Long crossings over seas, deserts or high mountain ranges are not uncommon in species as diverse as wildfowl, waders, passerines and raptors (Newton, 2008). Different environments impose different constraints, forcing migrants to respond accordingly. At one end of the spectrum are journeys across oceans by some terrestrial or wetland birds that cannot feed *en route*, and avoid landing on the water to rest, leading to long non-stop flights (e.g., bar-tailed godwits *Limosa lapponica baueri* can fly continuously for ~10,000 km between Alaska and New Zealand; Gill et al., 2009). Slightly less constrained are birds crossing a region where they can stop to rest or to wait for better conditions, but in general cannot forage, such as the numerous passerines, raptors, and other species which migrate over the Sahara Desert (Klaassen et al., 2008; Strandberg et al., 2009; Lemke et al., 2013). Finally, birds sometimes have to fly over moderately challenging barriers, i.e., areas where they can stop to rest and even find some food, but that are not suitable for long periods of residency; this applies to non-tropical seabirds migrating over equatorial oceans where marine productivity and wind speeds are consistently low (Mann and Lazier, 2005). The extent to which migrating birds must adapt their daily routines when crossing unfavourable habitats should depend on the ratio of energy accumulated while feeding to energy spent on travel (Strandberg and Alerstam, 2007).

It might seem intuitive that birds should spend more time in flight during migration than at other times of year, particularly when foraging conditions are unfavourable, as is the case for many terrestrial and wetland birds (Newton, 2008). Flying seabirds, in contrast, mostly search for food while on the wing and regularly commute between ephemeral food patches (Weimerskirch, 2007). Consequently, they might maintain the same bearing towards their ultimate non-breeding destination, but forage *en route* and not necessarily increase flying time during migration. Additionally, as seabirds can make efficient use of predictable winds over large scales (Felicísimo et al., 2008; Weimerskirch et al., 2017), they may not need to greatly increase flying time during migration. As most seabirds can land on water anywhere, and at any time, with low risk of predation,

they may show less propensity for long non-stop flights than other migratory birds. Although seabirds include some iconic long-distance migrants, such as the Arctic tern *Sterna paradisaea*, which migrates from Arctic breeding sites to spend the non-breeding season in the Southern Ocean (Egevang et al., 2010), we know relatively little about how these journeys are structured. However, there is evidence in just a few species of greater flight time during migration than in the rest of the non-breeding period (Mackley et al., 2010; Yamamoto et al., 2010; Dias et al., 2012a; Clay et al., 2017; Weimerskirch et al., 2020), and of longer flight bouts, although still only ca. 1–2 h (Mackley et al., 2011; Dias et al., 2012a; Clay et al., 2017).

The optimal time of the day to travel, feed, or rest can vary throughout the annual cycle depending on constraints mediated to some extent by light levels, which affect food detectability and availability, predation risk, wind conditions, and navigational cues. Seasonal and diel variation in such constraints affect the flight budgets of different species. Terrestrial bird species may either migrate exclusively at night (e.g., many passerines; Biebach et al., 2000), only during daylight (e.g., many raptors using thermal soaring; Strandberg et al., 2009), or use a combined strategy (e.g., when flying over ecological barriers; Alerstam, 2009; Adamik et al., 2016). Similarly, seabirds may concentrate most of their flight time during the day (e.g., breeding albatrosses, Phalan et al., 2007), be active both in daylight and darkness (e.g., white-chinned petrels *Procellaria aequinoctialis*, Mackley et al., 2011), or fly primarily at night (e.g., several petrels, Navarro et al., 2013; Dias et al., 2016; Rayner et al., 2016). Even within species, the degree of nocturnality can vary with environmental conditions (Dias et al., 2012b). Such flexibility suggests a high potential for adaptation of daily rhythms to the additional challenges faced during migration (e.g., crossing of unfavourable areas). A few studies have found evidence of seabirds becoming more nocturnal in their flight activity (Dias et al., 2012a; Hedd et al., 2012; Fayet et al., 2020), and that nocturnal flight bouts are longer during migration than in the non-breeding period (Mackley et al., 2011; Dias et al., 2012a; Clay et al., 2017). However, little is known about the extent to which most seabirds adjust their diurnal and nocturnal flight schedules while migrating, despite the useful insights it would provide into the challenges faced during this energetically demanding phase of the annual cycle.

Some of the differences in activity between day and night can be explained by light levels, and these are partially moderated by moonlight. A few studies based on landings of migrants or mist-netting suggest an influence of the lunar cycle on migratory intensity in terrestrial birds (Pyle et al., 1993; James et al., 2000; Speicher et al., 2011). However, the effect is well documented only in the European nightjar *Caprimulgus europaeus*, in which synchronous movements occurred 11 days after full moon - attributed to better foraging conditions during full moon and the time it takes to reach the ideal departure fuel load (Norevik et al., 2019). In seabirds, lunar influences on aerial activity have been mostly demonstrated in relation to foraging (Phalan et al., 2007; Yamamoto et al., 2008; Mackley et al., 2011; Dias et al., 2016; Pastor-Prieto et al., 2019), as moonlight can influence both prey availability (Regular et al., 2011) and prey detectability (Cruz et al., 2013). However, return to the colony of migrant Barau's petrel *Pterodroma barauii* appeared to be regulated by moonlight (Pinet et al., 2011), and Cory's shearwaters fly more and are more nocturnal on moonlit nights during migration (Dias et al., 2012a).

The increasing availability of tracking data in recent decades has provided opportunities to address fundamental questions relating to the scheduling of seabird flight activity and the effect of the moon. Two types of data are of particular interest and can be provided by the same small devices (light-level geolocators) throughout the non-breeding season: ambient light levels can be used for geolocation (providing longitude from the timing of local noon, and latitude from day length), and salt-water immersion can be used to determine timing and duration of flights (i.e., when loggers are dry). These loggers have been deployed widely on seabirds in the past 1–2 decades, shedding light on the migration patterns of many species (see **Supplementary Table 1** for examples). Here, we take advantage of tracking and immersion data from 526 individuals of 21 species from six families to understand (1) how seabirds adapt their behaviour during migration, and in particular whether they change (a) their overall time in flight, and (b) ratios of total flight in daylight vs. darkness; and (2) whether moon illuminance is associated with flight activity during migration. We compare activity patterns during migration (here defined as the long-distance directed movements to and from wintering grounds), to those during the non-breeding period (here defined as the time spent resident in the main non-breeding areas), as during the latter, birds are less constrained than in other parts of the annual cycle (e.g., during breeding, when they have to return to colonies to incubate or provision their young; Phillips et al., 2017).

MATERIALS AND METHODS

We collated geolocation (twice-daily positions at local midday and midnight) and salt-water immersion data (providing the timing and duration of flights and landings) for 21 migratory seabird species, collected using British Antarctic Survey (Cambridge, United Kingdom), Biotrack (Wareham, United Kingdom) or Intigeo (Cambridge, United Kingdom)

loggers deployed on adults at 27 different colonies. For original papers detailing fieldwork and processing methods, and number of individuals, year, and moon phase, see **Supplementary Tables 1, 2**. We focused on pelagic species for which these data were available year-round. Other taxa were excluded because they are often terrestrial during the non-breeding season (e.g., most gulls), or are pelagic but rest on floating objects - including ice - at sea [terns, Antarctic petrel *Thalassoica antarctica* (Delord et al., 2020) and giant petrels *Macronectes* spp.], or hold one leg out the water while resting (some alcid, Fayet et al., 2016), all of which affect apparent flight duration as measured using immersion loggers. In addition, analyses were restricted to long-distance migrants in which there were clear migration phases that could be separated from time spent in the non-breeding area, and for which the spatial error associated with geolocation (around 190 km; Phillips et al., 2004) was not a major issue. At least part of the migration phases also had to occur outside of the period around the equinoxes when latitude is difficult or impossible to estimate from light data (Hill, 1994). Procellariidae (shearwaters and petrels) are therefore better represented in our dataset than other families.

Definition of Migratory Periods

Migratory periods were defined for each bird based on dates provided by data owners, corresponding to those when the bird (1) left the breeding area, (2) arrived at the non-breeding grounds, (3) left the non-breeding grounds, and (4) returned to the breeding area. If these dates were not provided, we identified them manually for each individual using the time series of longitude, latitude or distance from the breeding area, associating approximately constant values of all these variables to non-breeding areas. Only data from the migration and non-breeding periods were included in analyses. Time series of distance to the breeding colony, colour-coded by migratory periods, are available in **Supplementary Materials (Supplementary Figure 1)**.

Definition of Daylight vs. Darkness and Moon Parameters

For each bird location (available twice-daily), we obtained the timings of civil twilights (times when the sun is 6° below the horizon) using the *crepuscule* function in the package *maptools* (Bivand and Lewin-Koh, 2018) in R (R Core Team, 2019) and used these values to separate activity into daylight (time between civil dawn and civil dusk) and darkness (time between civil dusk and civil dawn). For each bird location, we also calculated the illuminated fraction of the moon using the *moonAngle* function in the *oce* R package (Kelley and Richards, 2021). We then grouped values of illuminated fraction of the moon into three phases (new moon: between none and a third of the moon illuminated, quarters: between a third and two thirds of the moon illuminated, and full moon: between two thirds and all of the moon illuminated, similar to Dias et al., 2012a). No daylight-darkness or lunar phase values could be calculated around equinoxes as estimated latitudes during this period are unreliable; therefore, corresponding data were removed from the analyses.

Flight Budgets

We determined flight patterns from salt-water immersion data. For most species, the loggers tested for immersion at 3-s intervals and recorded the sum of positive tests (a value x from 0 to 200) at the end of each 10 min-period. The exception were the loggers used on Leach's storm petrels *Oceanodroma leucorhoa*, which sampled for immersion every 30 s but also binned the data into 10 min intervals, and the loggers used on Cory's shearwaters, which recorded the timing of every change of state from wet to dry, or *vice versa*, of ≥ 6 s. We considered time on the water to be the percentage of time in each 10 min bin in which the logger was wet, i.e., $x/200$. Similarly, flight time was calculated as the percentage of time in each 10 min bin in which the logger was dry, i.e., $(200-x)/200$. We then calculated the mean flight time during daylight and darkness for each individual. We considered flight bouts as any continuous sequence of one or more 10 min intervals in which the logger was fully dry, following Phalan et al. (2007). As flight bouts are included regardless of their duration (min. 10 min, as this is the resolution of the data), this approach did not allow us to distinguish between commuting flight during migration, and flight associated with foraging.

Night Flight Index

We calculated a Night Flight Index (NFI; an index of nocturnal flight activity) for each day (consecutive daylight and darkness period) following Dias et al. (2012a):

$$NFI = \frac{\%F_N - \%F_D}{\max(\%F_N, \%F_D)}$$

where $\%F_N$ = % of darkness time spent in flight, and $\%F_D$ = % of daylight time in flight. Percentages of time were used instead of absolute values in order to control for the effect of changing photoperiod at different latitudes during the year. This index varies between -1 when all the flight activity each day occurs in daylight (hereafter called "diurnal" behaviour), and 1 when all the flight activity takes place in darkness (hereafter called "nocturnal" behaviour). We mapped this index in space by calculating daily locations for each individual (average latitudes and longitudes of the two daily locations) and associating these with the daily NFI values. These spatially referenced individual daily locations were then overlaid in an Icosahedral Snyder Equal Area Aperture 3 Hexagon Discrete Global Grid (resolution 6), and values averaged per grid cell.

Statistical Analyses

We tested whether activity patterns differed during periods spent on migration and in the non-breeding grounds, or during the different phases of the lunar cycle, by modelling daily activity metrics separately for each species using Linear Mixed Models (LMMs) using the R package *nlme* (Pinheiro et al., 2021), with individual and time block within individual as random effects. Time blocks correspond to consecutive days of the same breeding stage and moon phase, and were included in the analysis to control for temporal autocorrelation. We analysed the following response variables: (1) % of time in flight, (2) flight bout durations, and (3) NFI. For ease of interpretation,

we split our dataset into new moon, moon quarter and full moon, and into daylight and darkness [for (1) and (2) only]. We then tested the effect of the migratory phase (with the non-breeding period as a reference) separately for each sub-dataset. Similarly, we split our dataset into outward or return migration, and the non-breeding period, and between darkness and daylight [for (1) and (2) only]. We then tested separately the effect of moon phase (with new moon as a reference) for each sub-dataset. Also for ease of interpretation, we contrasted only new moon and full moon phases to test for the effect of moon phase. Variables were transformed as follows before fitting the models: proportion of time in flight was logit-transformed, flight bout duration was log-transformed, and the NFI was rescaled between 0 and 1 [i.e., $(NFI + 1)/2$] and logit-transformed. Unless stated otherwise, we obtained single values per species (e.g., percentage of flight time over a certain migratory period, or a certain moon phase) by averaging values across days (separating daylight and darkness, where appropriate) for each individual, and then we used the mean of those values in posterior analyses. The percentage of time spent in flight and the NFI each day during migration (outward and return migrations separately) in relation to the percentage of time in flight during the non-breeding period was compared between transequatorial and non-transequatorial migrant species (classified according to the movements of the majority of individuals, see **Supplementary Table 2** for details).

All calculations of flight budgets, mapping and analyses were carried out using the R statistical software.

RESULTS

General Flight Activity Patterns

All species spent more time in flight and had longer flight bouts during at least one migration period (outward, return, or both) than in their non-breeding areas (**Tables 1, 2, Figures 1, 2A–C, Supplementary Figure 2**). This increased flight time occurred during both daylight and darkness (**Figure 1**), with the magnitude of the change varying markedly among species (**Figure 2C**). The ratio of flight time during migration to flight time during the non-breeding period varied from 1.16 in black-legged kittiwakes *Rissa tridactyla* to 4.63 in short-tailed shearwaters *Ardenna tenuirostris* (based on mean values, **Supplementary Table 3** and **Figure 2C**). For reference, **Supplementary Table 3** also provides latitudinal migratory range and migratory distance (here defined as distance between breeding and non-breeding range) for each species. Median flight bout duration rarely exceeded a few hours (**Table 2**). However, a few individuals of some species (great shearwaters *Ardenna gravis*, short-tailed shearwaters, red-tailed tropicbirds *Phaethon rubricauda*, south polar skuas *Stercorarius maccormicki*, long-tailed skuas *Stercorarius longicaudus* and black-legged kittiwakes) performed bouts > 24 h, mostly during migration (**Supplementary Table 4**).

Despite the higher flight activity, most species spent a considerable amount of time on the water during migration (from 17% in Murphy's petrel *Pterodroma ultima* during outward migration to 78% in south polar skua during return migration)

TABLE 1 | Mean (\pm SD) percentage of time spent in flight during each migratory stage for different seabird species.

		Outward migration	Non-breeding period	Return migration
Great shearwater	<i>Ardenna gravis</i>	76.6 \pm 19.6	28.9 \pm 21.3	67.1 \pm 22.9
Sooty shearwater	<i>Ardenna grisea</i>	72.2 \pm 19.3	23.9 \pm 15.2	67 \pm 24.1
Flesh-footed shearwater	<i>Ardenna carneipes</i>	69.9 \pm 19.7	33.0 \pm 22.0	77.7 \pm 20.0
Short-tailed shearwater	<i>Ardenna tenuirostris</i>	75.4 \pm 24.6	20.0 \pm 17.5	75.9 \pm 22.6
Manx shearwater	<i>Puffinus puffinus</i>	43.0 \pm 23.9	18.6 \pm 9.9	52.2 \pm 26.5
Cory's shearwater	<i>Calonectris borealis</i>	51.8 \pm 19.9	25.9 \pm 15.1	57.1 \pm 19.9
Cape Verde shearwater	<i>Calonectris edwardsii</i>	45.0 \pm 21.1	15.2 \pm 11.1	48.2 \pm 21.8
White-chinned petrel	<i>Procellaria aequinoctialis</i>	71.2 \pm 22.2	27.5 \pm 15.6	69.4 \pm 17.6
Bulwer's petrel	<i>Bulweria bulwerii</i>	66.7 \pm 9.2	56.6 \pm 7.4	77.9 \pm 8.5
Pycroft's petrel	<i>Pterodroma pycrofti</i>	56.0 \pm 16.2	33.0 \pm 15.7	58.0 \pm 21.3
Murphy's petrel	<i>Pterodroma ultima</i>	83.1 \pm 13.7	39.9 \pm 19.3	80.8 \pm 12.8
Barau's petrel	<i>Pterodroma barau</i>	79.0 \pm 11.8	41.3 \pm 16.6	59.9 \pm 16.5
Cook's petrel	<i>Pterodroma cookii</i>	76.8 \pm 16.3	36.0 \pm 16.3	73.1 \pm 15.3
Black-winged petrel	<i>Pterodroma nigripennis</i>	66.5 \pm 18.1	51.0 \pm 20.1	76.9 \pm 10.0
Buller's albatross	<i>Thalassarche bulleri</i>	76.7 \pm 19.4	30.9 \pm 17.6	66.4 \pm 19.2
Black-browed albatross	<i>Thalassarche melanophris</i>	36.5 \pm 23.5	32.8 \pm 18.8	50.0 \pm 19.0
Leach's storm petrel	<i>Oceanodroma leucorhoa</i>	71.0 \pm 12.5	49.6 \pm 11.9	62.4 \pm 12.6
Red-tailed tropicbird	<i>Phaethon rubricauda</i>	39.4 \pm 12.4	25.4 \pm 9.8	26.3 \pm 11.8
South polar skua	<i>Stercorarius maccormicki</i>	34.3 \pm 19.7	12.2 \pm 8.5	22.1 \pm 20.9
Long-tailed skua	<i>Stercorarius longicaudus</i>	47.3 \pm 25.5	26.3 \pm 17.2	37.3 \pm 21.1
Black-legged kittiwake	<i>Rissa tridactyla</i>	35.6 \pm 15.1	31.3 \pm 10.5	46.3 \pm 19.6

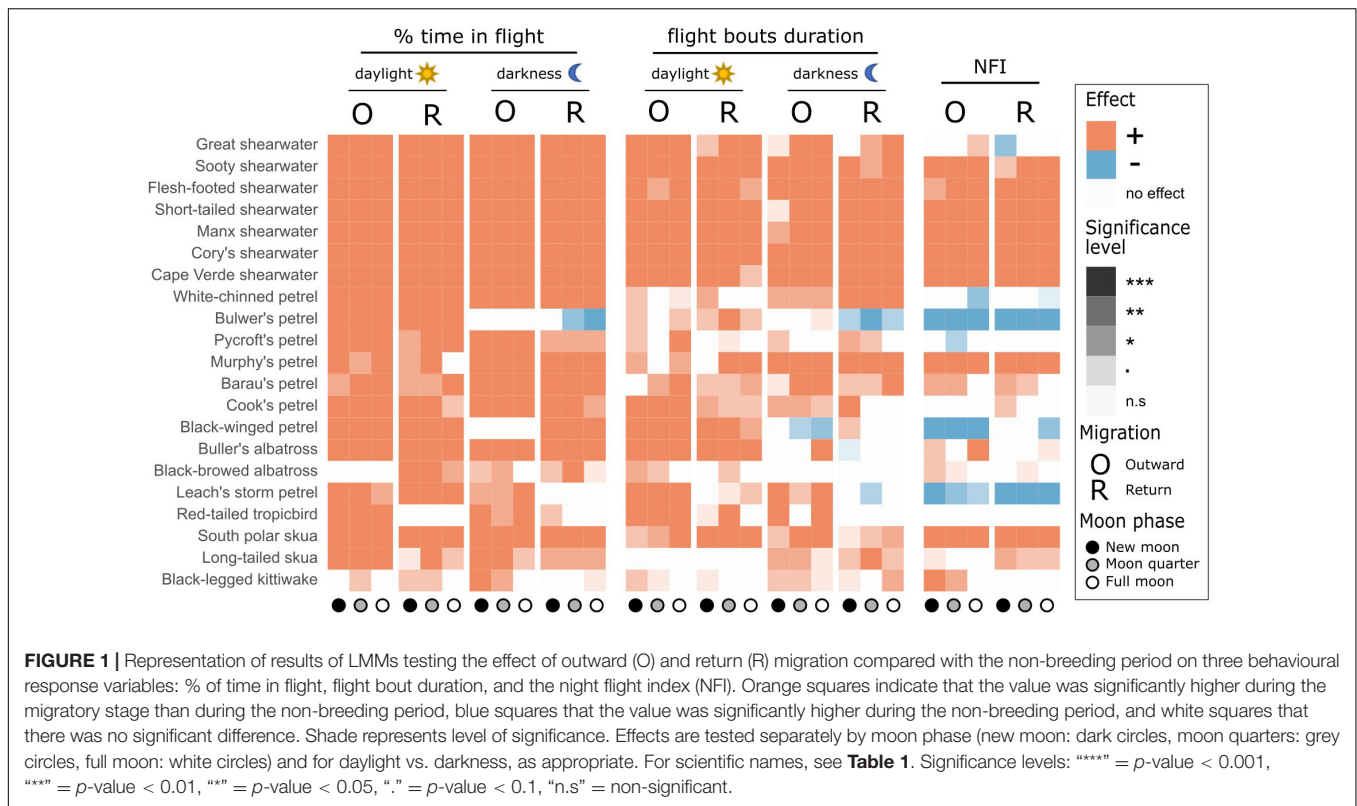
Values based on the means for individual tracks. Percentage of time spent on the water is 100% minus percentage of time in flight. Species ordered according to phylogenetic proximity. See **Figure 1** for the results of statistical tests contrasting times in flight between migrations and the rest of the non-breeding period.

TABLE 2 | Flight bout duration (in hours) during each migratory stage.

		Outward migration	Non-breeding period	Return migration
Great shearwater	<i>Ardenna gravis</i>	2.83 [6.17]	2.00 [5.17]	3.00 [6.67]
Sooty shearwater	<i>Ardenna grisea</i>	2.98 [8.17]	1.50 [4.33]	3.35 [9.00]
Flesh-footed shearwater	<i>Ardenna carneipes</i>	2.89 [5.17]	1.50 [4.17]	2.33 [4.83]
Short-tailed shearwater	<i>Ardenna tenuirostris</i>	3.67 [6.83]	2.17 [6.00]	5.13[12.83]
Manx shearwater	<i>Puffinus puffinus</i>	2.03 [3.83]	1.17 [3.17]	2.50 [6.42]
Cory's shearwater	<i>Calonectris borealis</i>	0.79 [6.29]	0.26 [3.92]	1.03 [5.74]
Cape Verde shearwater	<i>Calonectris edwardsii</i>	2.04 [3.83]	1.50 [3.50]	2.45 [4.25]
White-chinned petrel	<i>Procellaria aequinoctialis</i>	1.85 [4.01]	1.67 [5.18]	2.00 [4.50]
Bulwer's petrel	<i>Bulweria bulwerii</i>	1.36 [2.75]	1.33 [4.08]	1.01 [3.58]
Pycroft's petrel	<i>Pterodroma pycrofti</i>	1.50 [3.25]	1.25 [4.25]	1.55 [3.67]
Murphy's petrel	<i>Pterodroma ultima</i>	2.50 [5.33]	1.67 [4.33]	3.18 [7.33]
Barau's petrel	<i>Pterodroma barau</i>	2.67 [4.83]	2.00 [6.00]	2.62 [5.25]
Cook's petrel	<i>Pterodroma cookii</i>	1.83 [5.83]	1.33 [4.00]	1.75 [3.44]
Black-winged petrel	<i>Pterodroma nigripennis</i>	1.83 [5.33]	1.67 [5.67]	1.83 [4.00]
Buller's albatross	<i>Thalassarche bulleri</i>	3.24 [5.33]	1.67 [4.75]	2.34 [6.27]
Black-browed albatross	<i>Thalassarche melanophris</i>	3.35 [4.85]	3.65 [10.24]	3.71 [5.58]
Leach's storm petrel	<i>Oceanodroma leucorhoa</i>	2.00 [5.67]	1.42 [4.42]	1.17 [3.00]
Red-tailed tropicbird	<i>Phaethon rubricauda</i>	3.39 [8.33]	2.17 [8.08]	2.17 [4.58]
South polar skua	<i>Stercorarius maccormicki</i>	2.46 [12.33]	1.25 [4.33]	2.17[11.00]
Long-tailed skua	<i>Stercorarius longicaudus</i>	6.47 [12.67]	4.83 [11.33]	7.15[11.25]
Black-legged kittiwake	<i>Rissa tridactyla</i>	2.17 [4.33]	1.83 [7.00]	2.13 [4.67]

Values are the medians across individuals of individual 95% quantile, with maximum values across individuals of 95% quantile between square brackets. Species ordered according to phylogenetic proximity. See **Figure 1** for the results of statistical tests contrasting flight bout durations between migrations and the rest of the non-breeding period.

(**Table 1**). In many species, a high percentage of time on the water during migration occurred in bouts > 1 h [median across species of 40.0% (outward)/46.4% (return), with minima of 15.8% (outward)/7.5% (return) for Bulwer's petrel *Bulweria bulwerii* and maxima of 78.3% (outward)/84.6% (return) for black-browed albatrosses *Thalassarche melanophris*; **Supplementary Table 5**].



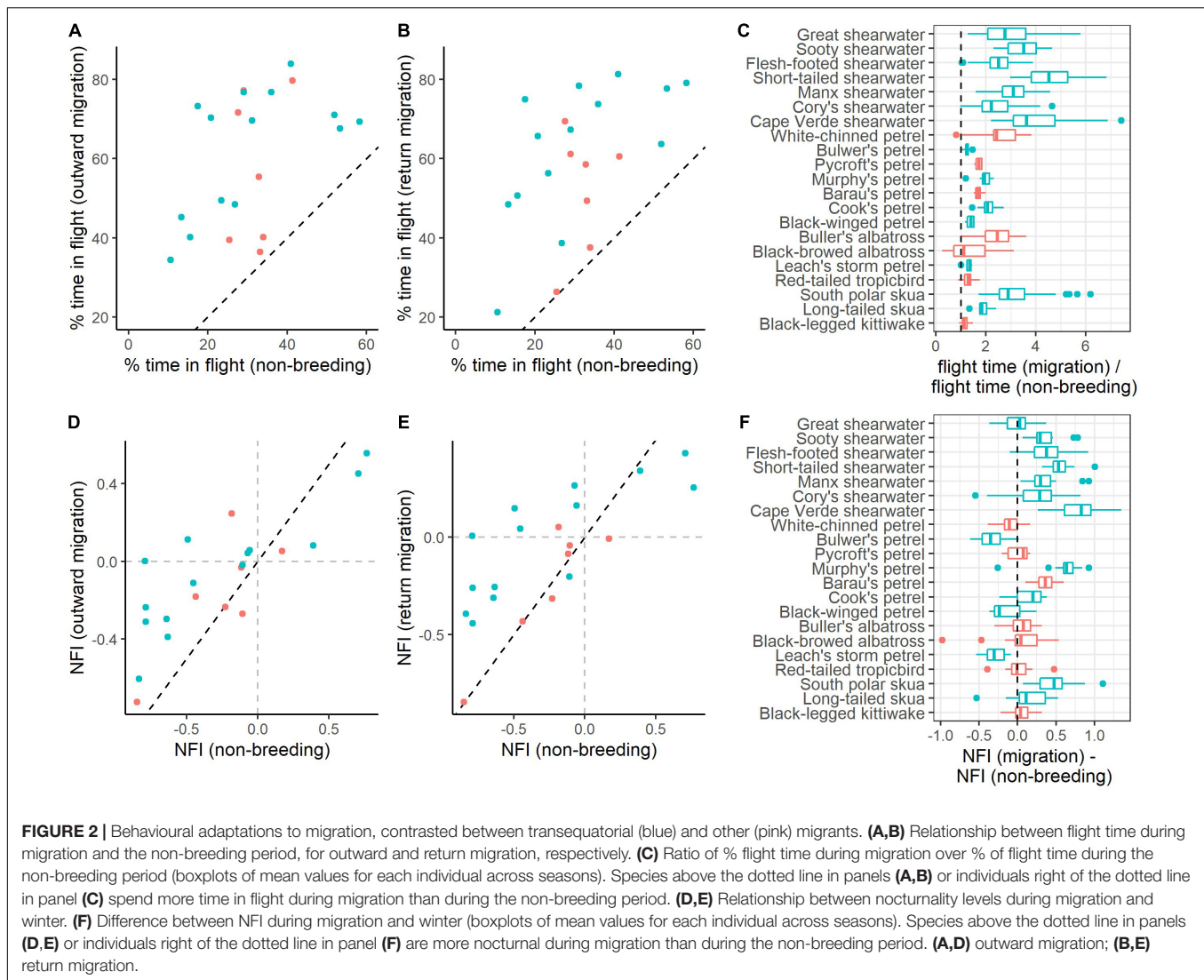
During the three consecutive days with the greatest flight activity (hereafter termed the “peak migration period”), many species spent 80–90% of the time in flight, indicating they nevertheless rested for at least 2 h per day (**Figure 3**). However, there were several species that spent substantially less time in flight: for example, the proportions of time spent in flight in these three days during the outward and return migrations (median values across individuals) were only 67 and 65% in Cape Verde shearwaters *Calonectris edwardsii*, 53 and 65% in the mostly diurnal, black-legged kittiwakes, and 57 and 46% in red-tailed tropicbirds, respectively. Even when crossing equatorial regions, species often spent less than 75% of their time in flight, although this varied among transequatorial migrants: skuas often spent <50%, whereas *Puffinus* and *Ardenna* shearwaters spent most time in flight (**Supplementary Figure 3**).

Daily Activity Budgets During Migration

During both migration and the non-breeding period, all species flew during both daylight and darkness, although there was a large variation in baseline (non-breeding period) NFI values among species (**Figures 4, 5** and **Supplementary Table 6**). The most diurnal species during the non-breeding period was the black-legged kittiwake (baseline NFI: -0.8 ± 0.3), followed by the south polar skua (-0.8 ± 0.4) and most shearwaters, and then the two albatross species (-0.4 ± 0.5 and -0.2 ± 0.6). Only four species were predominantly nocturnal during the non-breeding period: Bulwer’s petrel (0.8 ± 0.2), black-winged petrel *Pterodroma nigripennis* (0.4 ± 0.3), Leach’s storm-petrel (0.7 ± 0.2) and to a lesser extent, white-chinned petrel (0.2 ± 0.6).

For several species – both diurnal (e.g., the two skuas) and nocturnal (e.g., Bulwer’s petrel) – mean flight bout duration was longer in darkness than in daylight [comparison between individual daily means of flight bout duration in darkness vs. in daylight, paired t -test, all species combined: mean difference (in hours): 0.036, $t = 7.779$, $df = 45181$, $p < 0.001$; **Supplementary Figure 4**].

Most species were more nocturnal (i.e., increased NFI, mostly through a greater increase in time in flight during darkness than daylight) in the migration than non-breeding periods, but there were exceptions (**Figures 1, 2D–F**). In particular, the four species that were predominantly nocturnal at their non-breeding grounds (Bulwer’s petrel, black-winged petrel, Leach’s storm petrel, and white-chinned petrel) showed a reverse trend and became more diurnal during migration (i.e., there was a greater increase in time in flight during daylight than darkness; **Figure 1**). NFI changed little in other species, including those that were not clearly more diurnal or more nocturnal at their non-breeding grounds (i.e., cathemeral), but also a few that were clearly diurnal, such as albatrosses (**Figures 1, 4**). Transequatorial migrants appeared to be more diurnal at higher latitudes (where most species spent the non-breeding period), and more nocturnal in equatorial regions (**Figure 6**). This pattern was consistent across several families. However, in certain regions such as the Indian Ocean, some species appeared more diurnal around the tropics (**Figure 6**), which might suggest the presence of pelagic prey communities of a different nature (i.e., with more epi-pelagic and fewer mesopelagic prey), but more research will be needed to confirm this speculation.



Influence of Moon Phases

For many species there was increased nocturnal activity with increased moonlight in at least one period (during migration and/or when in non-breeding areas), with the exception of the Manx shearwater *Puffinus puffinus*, Pycroft's petrel *Pterodroma pycrofti*, and Leach's storm petrel (Figure 7). The mostly nocturnal Bulwer's petrel showed different responses to the moon across the year: more nocturnal in full moon in the non-breeding areas, and the reverse during return migration (Figure 7 and Supplementary Figure 5). Several species that increased their NFI during full moon also reduced their activity in daylight (Figure 7 and Supplementary Figure 6B). This compensation was clear during migration, but was not apparent in non-breeding areas (Supplementary Figure 6B; paired *t*-test across species comparing the moon effect during daylight in the non-breeding areas vs. during migration: mean difference: -2.54 , $t = -2.33$, $df = 20$, $p = 0.031$). There was no indication that the effect of moon phase on the NFI was more pronounced during migration (Supplementary Figure 6A; paired *t*-test across

species: mean difference: 0.06 , $t = 1.67$, $df = 20$, $p = 0.110$). Lunar phases had a similar effect on predominantly nocturnal and predominantly diurnal species (Supplementary Figure 6A; small effect during migration, no effect during the non-breeding period, Supplementary Table 7).

DISCUSSION

Using an extensive dataset on movements and flight behaviour of 21 species from six families, we show how flying seabirds adapt their flight budgets to migration, and the influence of the moon. In general, time in flight, and in several species also flight bout duration, increased during migration, but the extent varied among species. Nevertheless, all species spent some time resting, even on the three days when flight activity peaked. Virtually all species adjusted their diel activity schedules during migration. We found some influence of the lunar phase on flight activity, but that was not necessarily more pronounced

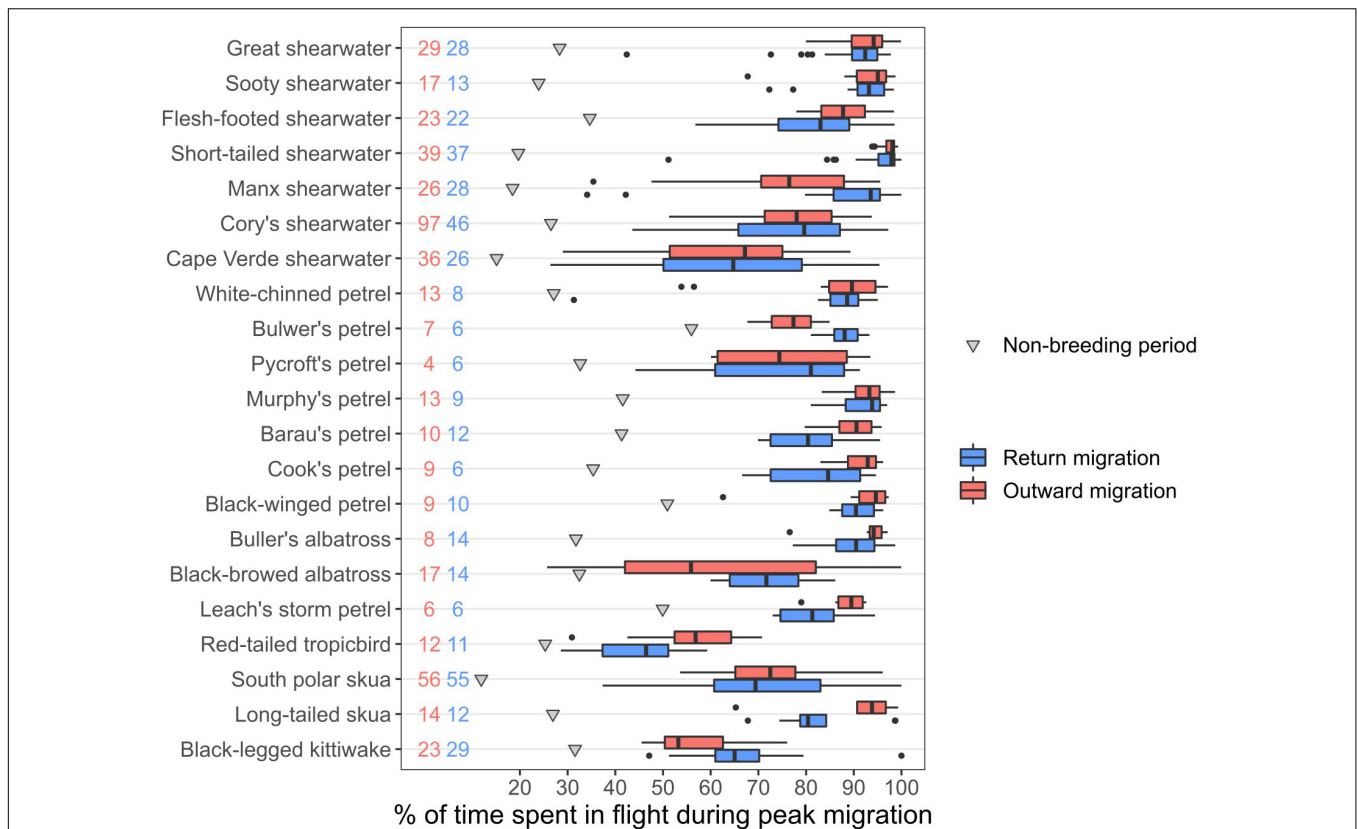


FIGURE 3 | Percentage of time spent in flight during the three consecutive days with the highest flight activity for each individual, aggregated by species. Pink: outward migration, blue: return migration, grey triangles: average flight time during the non-breeding period, for reference. Black dots represent outliers of the boxplots. Numbers represent sample sizes (pink: outward migration, blue: return migration).

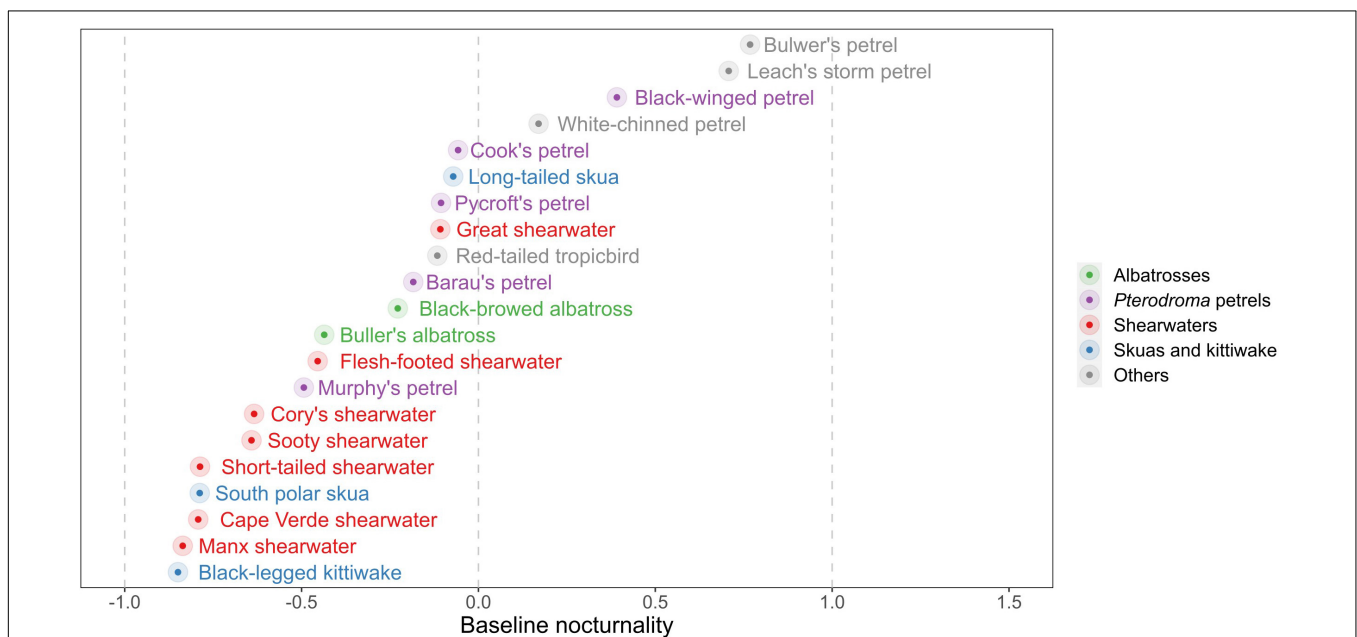
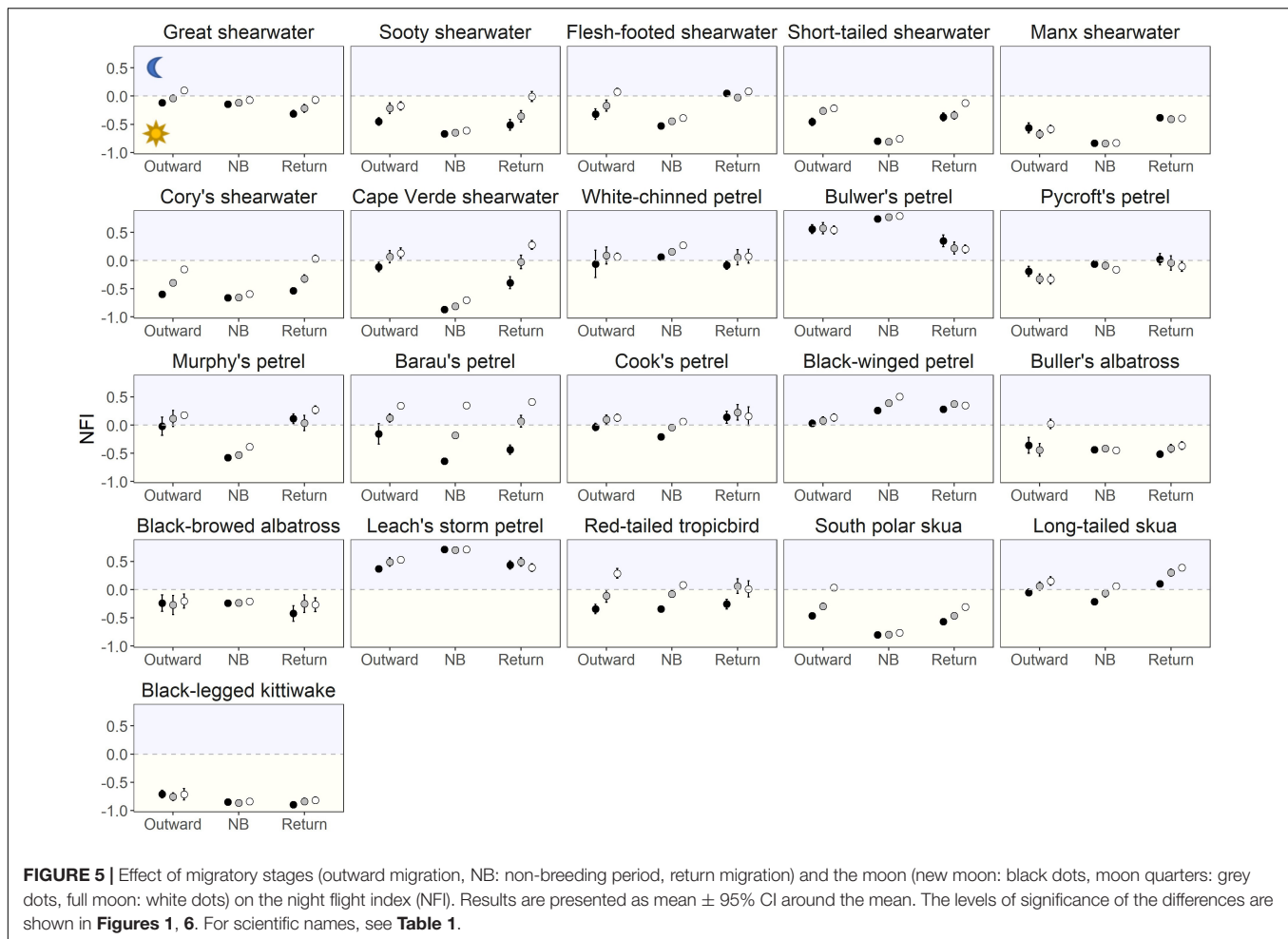


FIGURE 4 | Night flight index during the non-breeding period averaged across days and individuals (coloured dots). Negative values correspond to diurnal species (i.e., species which fly more during daylight than darkness), while positive values are for nocturnal species (i.e., species which fly more during darkness than daylight). For exact values and standard deviations, see **Supplementary Table 5**.

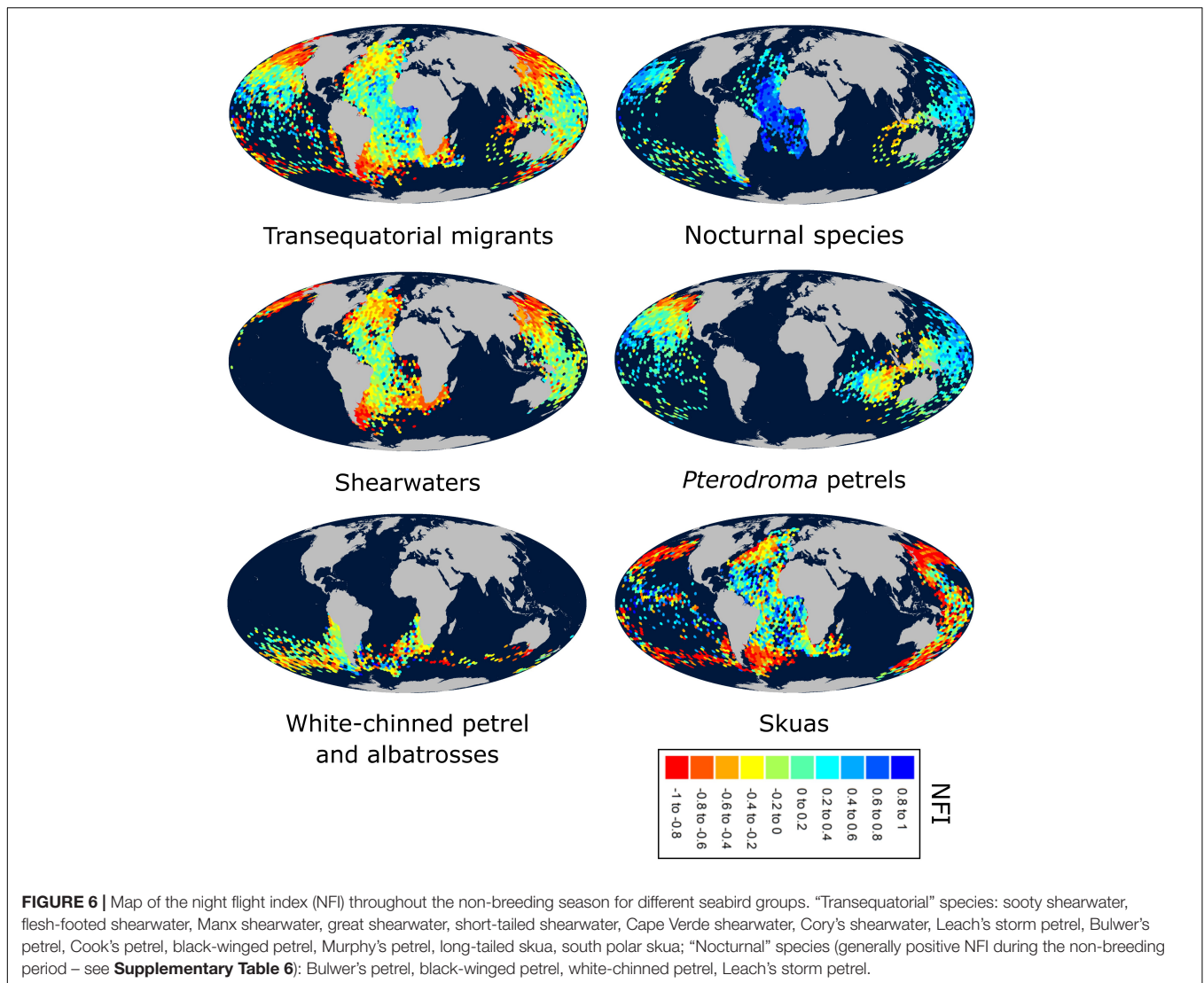


during migration than when birds were resident in their non-breeding areas.

Our study had broad taxonomic scope, yet we found a consistent increase in daily flight time during migration across species (and most pronounced among shearwaters) often two to three times higher than observed during the non-breeding period. This increase in flight time during migration suggests that all the study species were motivated to move faster over certain environments, possibly because these are less favourable habitats for foraging. This observed increase is consistent with results from species not studied here: the wedge-tailed shearwater *Ardenna pacifica* (Weimerskirch et al., 2020) and, to a lesser extent, several albatross species (Mackley et al., 2010; Gutowsky et al., 2014). For some species (e.g., most shearwaters), we also found an increase in flight bout duration during migration, which has also been observed in albatrosses (Mackley et al., 2010). Hence, our study shows that during migration, seabirds do not simply retain the same routine (for example, adjusting flight direction towards the preferred non-breeding region), but instead that they routinely change their flight budgets. Note that birds may fly less when resident at non-breeding grounds because of primary moult impairing flight capabilities (Tucker, 1991; Bridge, 2003; Cherel et al., 2016). However, the many gaps in knowledge

of the timing of moult in seabirds (Bridge, 2007) prevent us from clearly attributing reduced flight activity to moult. In any case, many birds, including seabirds, avoid moulting during migration (e.g., Ramos et al., 2009), which may be a strategic choice in order to maintain high flight capability.

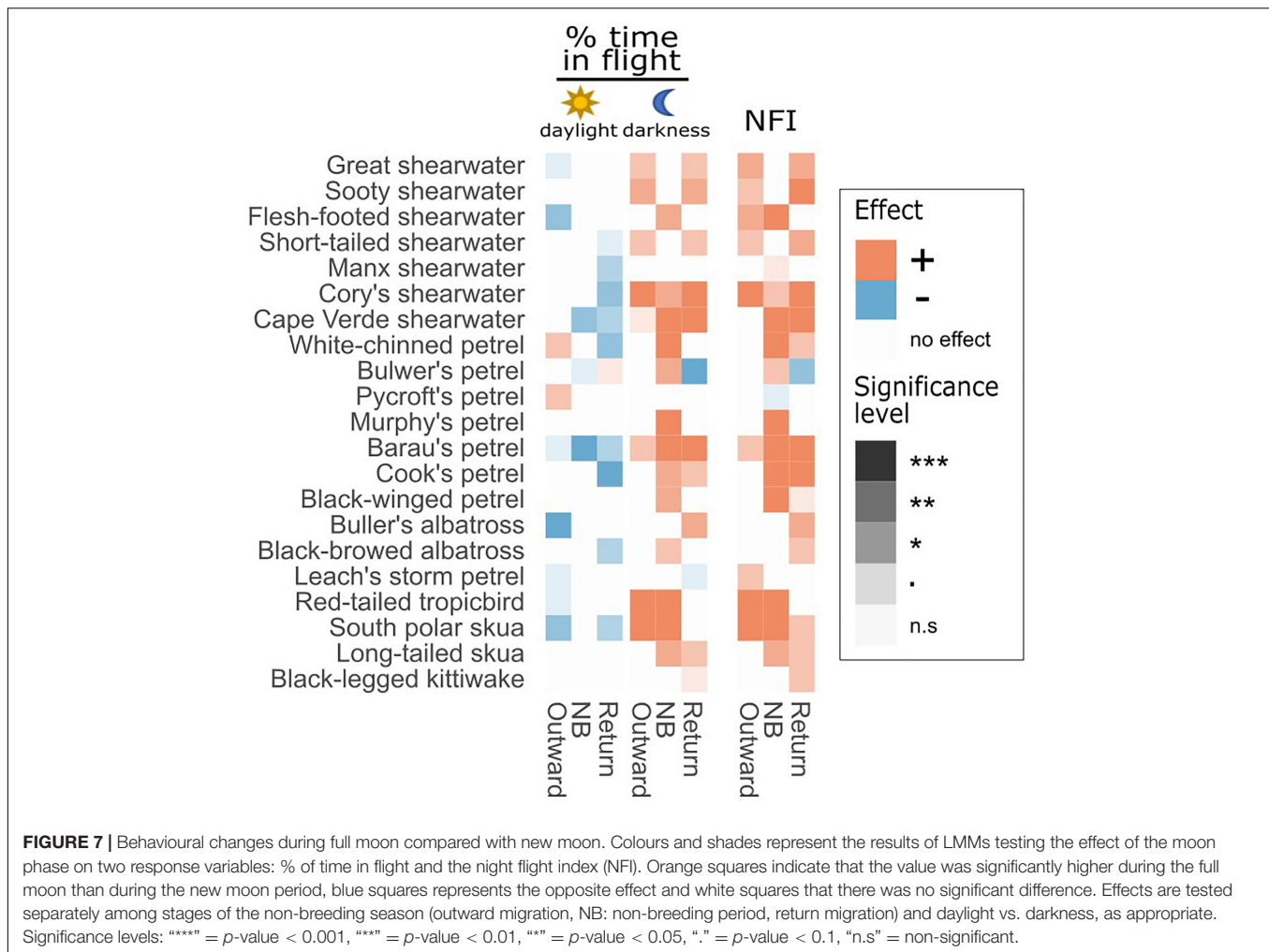
Our study provided a quantitative analysis of nocturnality, in the form of the Night Flight Index, which could be compared readily among species and periods. Most species that were diurnal in their non-breeding areas (i.e., when foraging without central-place or migration constraints) were also diurnal during both the outward and return migrations, and the opposite was true for species that were nocturnal in their non-breeding areas. However, regardless of the degree of nocturnality in the non-breeding period, the flight bouts of most species were longer in darkness than daylight throughout the time away from the colony, suggesting that night is preferred for (long-distance) travel. Many species re-adjusted the degree of nocturnality during migration (flying more at night than in the rest of the non-breeding period). Species that were nocturnal in their non-breeding areas (**Figure 4**) showed the opposite pattern (**Figures 1, 2**). Although not tested formally, this general pattern was also apparent in diurnal albatrosses (Mackley et al., 2010), wedge-tailed shearwaters (Weimerskirch et al., 2020) and Manx



shearwaters (Fayet et al., 2020), and in the nocturnal Bugio petrel *Pterodroma deserta* (Ramírez et al., 2013). This suggests that seabirds adjust their flight time during the time of day when there is more scope for additional flight, which minimises the time spent travelling during the rest of the 24-h period when foraging is more profitable. The changes in nocturnality and the increase in overall flying time appeared particularly pronounced for non-tropical species migrating across the equator (e.g., all shearwaters except the great shearwater, as well as both skuas, **Figures 2, 6**). Although phylogeny and transequatorial migration were correlated in our sample, limiting the possibility of robust contrasts, this suggests that for non-tropical seabirds, equatorial waters act as a barrier that requires greater behavioural adjustments than crossing temperate or polar waters. This could be because equatorial waters are oligotrophic (Mann and Lazier, 2005), or because lower winds (i.e., doldrums; Lamb, 1975) make flight more challenging.

Although our results show that the studied seabirds increase their flight time during migration, the change is much less

pronounced than in some other birds, such as certain waders and passerines (Newton, 2008). Even during the three consecutive migratory days with the greatest time in flight, many seabirds still spent a large proportion of time on the water (**Figure 3**). In addition, predominantly nocturnal species increased diurnal flight activity before allocating the entirety of the remaining time available for flying at night, and the converse applied to predominantly diurnal birds (daylight or darkness time never filled 100% with flight, **Supplementary Figure 5**). This suggests that most seabirds avoid spending too much time flying (which may be costly), and prefer to stop regularly, even during migration (Landers et al., 2011; Mackley et al., 2011; Gutowsky et al., 2014; Berg et al., 2019; Weimerskirch et al., 2020, but see van Bemmelen et al., 2019). However, it is difficult to investigate directly the energetic implications of these different behaviours, creating an avenue for future research. Finally, compared with passerines or waders crossing unfavourable terrestrial or marine environments (Newton, 2008), our study species did not undertake very long flight bouts (rarely more



than a few hours; **Table 2**). This could suggest that long flight bouts would be very costly, although it is unlikely for soaring or gliding birds (Weimerskirch et al., 2000; Sakamoto et al., 2013), except in areas with particularly weak winds. Alternatively, long flight bouts could be unnecessary if food supply is adequate and weather conditions relatively benign, providing little incentive to proceed rapidly to non-breeding grounds.

Further evidence that seabirds are unwilling to greatly increase flight effort per day is the compensation observed in some species during full moon: birds that increased flight time during darkness, flew less during daylight. This suggests that when conditions allow, seabirds prefer to spread their flight effort over a wider period including darkness. Furthermore, even when crossing the equator, non-tropical seabirds spent a considerable amount of time on the water (**Supplementary Figure 3**), indicating benefits of stopping to rest (potentially because equatorial winds make flight more challenging), rehydrate, or refuel regularly during migration, even if foraging conditions might be suboptimal. Note that terrestrial and wetland species preparing for long migrations accumulate a large amount of fat (Schaub and Jenni, 2000; Krapu et al., 2006), even sometimes shrinking organs not used for migration (Piersma et al., 1999).

However, this behaviour is likely to be costly, so if it can be avoided by seabirds by simply stopping *en route* to feed and rest, they may be less challenged by migration.

Our approach did not allow us to discern exactly what birds are doing when they stop flying, but the periods when all study species alternated between very short flights and landings suggests regular foraging during migration (Dias et al., 2012a). This is likely to include time spent digesting prey while sitting on the water (Jackson, 1988; Ropert-Coudert et al., 2004). However, the existence of long wet bouts during migration (**Supplementary Table 5**) suggests that birds might also spend time resting between flight bouts geared towards long-distance travel. Taxa other than seabirds also halt their migratory journeys to rest, even when no food is available. For instance, Brent geese *Branta bernicla hrota* leave Iceland in spring with enough fuel to cross the Greenland ice cap but nevertheless stop regularly to rest while *en route* at sites with no food available (Gudmundsson et al., 1995). There is evidence that long migratory flights can lead to muscle damage (e.g., in western sandpiper *Calidris mauri* and bar-tailed godwits, Guglielmo et al., 2001), or oxidative stress (European robin *Erithacus rubecula*, Jenni-Eiermann et al., 2014). Finally, sleep might be important. Although white-crowned sparrows

Zonotrichia leucophrys gambelii can withstand sleep deprivation during migration (Rattenborg et al., 2004), and great frigatebirds *Fregata minor* can even sleep while on the wing (Rattenborg et al., 2016), it is unknown how ecologically relevant, widespread, and costly, these adaptations are. Many birds apparently need to sleep once they finish long migratory journeys (Schwilch et al., 2002; Németh, 2009; Covino and Cooney, 2015). Seabirds might therefore spend much of their time sleeping between flights, even during migration, to avoid the costs of sleep deprivation.

Almost all species showed increased flight activity during darkness, and increased nocturnality during the full moon for at least part of the year (Figure 7), but it is difficult to determine whether the lunar cycle has a greater influence on travel or foraging. For at least partly nocturnal foragers, intensified foraging effort on nights with a full moon may indicate they have to work harder as conditions are unfavourable, for example if prey performing diel vertical migration are less accessible, or conversely that foraging conditions are favourable (e.g., because of increased visibility) and that birds expend more effort because the returns are good (Mackley et al., 2011; Pinet et al., 2011; Cruz et al., 2013; Rubolini et al., 2015; Dias et al., 2016; Ravache et al., 2020). Such lunar influences on foraging activity, sometimes mediated by predator avoidance, have been reported in a wide range of taxa (Yamamoto and Trathan, 2015): not only in birds (Clarke, 1983; Evens et al., 2020), but also in insects (Kerfoot, 1967) and mammals (Fernandez-Duque, 2003; Penteriani et al., 2013). However, moon-mediated visibility could also affect travel, as darkness could hamper the manoeuvres used for dynamic soaring, as suggested by Dias et al. (2012b) to explain the stronger effect of the moon on the flight activity of Cory's shearwaters during migration than in the non-breeding residency period. Finally, it has been suggested in other organisms that the moon could help navigation [in insects, Baker (1987), Dacke et al. (2003, 2011) or crustaceans, Ugolini (2016)], although the considerable debate about the underlying mechanisms (detection of landmarks, moon compass or light-mediated magnetic compass, orientation using polarised light) (see Muheim and Jenni, 1999 for a review), and the extent to which they could apply to seabirds remains unknown. In our study, all configurations were observed (moon effect during migration only, the non-breeding period only, both, or neither; Figure 7), making a general interpretation difficult. Nevertheless, that many species showed an increase in flight bout duration during full moon (Supplementary Figure 4) suggests that bright moon illumination favours travel more than foraging.

Overall, this study provides the most comprehensive analysis to date of how seabirds adjust their activity budgets during migration, and highlights greater flexibility in their behaviour than that of terrestrial migrants. Indeed, while we found a general increase in flight activity during migration, all species took regular stops. Several species also adjusted their daily schedules to migration: diurnal species becoming more nocturnal, and *vice versa* for nocturnal species. Finally, moon phase affected the flight activity of many species, mostly increasing nocturnality, but the effect was similarly pronounced when birds were migrating and when in non-breeding areas. The study also raises new questions about the main drivers of the variation among species in daily

activity budgets during migration, the energetic implications of these changes in time budgets, and the effects of moon phase on travel and foraging in birds.

DATA AVAILABILITY STATEMENT

The data analysed in this study is subject to the following licenses/restrictions: Data requests should be sent directly to the authors. Requests to access these datasets should be directed to PC (paulo.catry@gmail.com) and will be redirected to the appropriate data holders.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study does not use newly collected data on vertebrate animals, but only re-uses already collected data, which received ethical approval at the time of collection.

AUTHOR CONTRIBUTIONS

PC, MPD, RAP, and JPG conceived the ideas and contributed to the writing. All authors except A-SB-L collected the data. A-SB-L and MPD analysed the data. A-SB-L led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.683071/full#supplementary-material>

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