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Nocturnal flight activity of northern gannets *Morus bassanus* and implications for modelling collision risk at offshore wind farms

Keywords: offshore wind farm, seabird, collision risk modelling, data logger, nocturnal flight activity

ABSTRACT

Assessing the potential impacts of proposed offshore wind farm developments on seabird populations requires estimation of nocturnal flight activity of seabirds for input into collision risk models. One of the seabirds considered most at risk from collision with offshore wind turbines is the northern gannet *Morus bassanus*. The recommended correction for gannet nocturnal flight activity is currently a highly precautionary value. Here we use data from tracking studies to derive evidence-based correction factors for nocturnal flight activity of adult gannets during the breeding and nonbreeding seasons, and of immature gannets during the summer prospecting phase. Flight and diving activity of gannets was minimal during the night, astronomical and nautical twilight, for adults during the breeding season and nonbreeding season, and for immatures. Some flight activity occurred during the short period of civil twilight, but on average at about half the level seen during the day. Based on evidence from numerous tracking studies, we recommend that precautionary values of the nocturnal (sunset to sunrise) flight activity factor for estimating collision risk should be 8% of daytime flight activity during the breeding season and 3% of daytime flight activity during the nonbreeding season. Use of these evidence-based correction factors will improve the accuracy, and reduce the uncertainty of collision risk models, providing a more reliable assessment of the impacts of offshore wind farms on gannets.

1. Introduction

One of the key environmental issues facing developers of offshore wind farms in Environmental Impact Assessments is the impact that turbines may have on seabird populations as a consequence of mortality of birds that collide with rotating blades (Garthe and Hüppop, 2004; Furness et al., 2013). Bird collision mortality can be estimated using the Band collision risk model (Band, 2012). However, this requires an estimate of nocturnal flight activity as one of the model inputs. Seabird surveys at proposed offshore wind farm sites do not record the numbers of birds flying through the area at night, as visual (boat-based counts) or photographic (aerial) surveys are only practical during daylight hours. It is, therefore, necessary to use a correction factor, relative to daytime data, to allow for nocturnal flight activity of seabirds. Garthe and Hüppop (2004) assigned nocturnal flight activity scores to seabird species in five categories (scores of 1 to 5), based on existing limited evidence, their own judgement, and that of a panel of experts. They indicated that a score of 1 represented *'hardly any flight activity at night'* while a score of 5 represented *'much flight activity at night'*. These scores simply indicated that bird species that scored higher were likely to show more nocturnal flight activity than bird species that scored lower on the scale. Nevertheless Band (2012) advocated an arbitrary but precautionary translation of the Garthe and Hüppop (2004) scores for collision risk modelling as follows:

- 1=0% of daytime flight activity,
- 2=25% of daytime flight activity,
- 3=50% of daytime flight activity,
- 4=75% of daytime flight activity,
- 5=100% of daytime flight activity.

It is important to note that these suggested percentages were not based on evidence. It is also clear from Garthe and Hüppop (2004) that many of the scores for other seabird sensitivity metrics that they assigned were categorical rather than linear. Explicit examples are their scoring of population size; 1=>3million, 2=1-3 million, 3=500,000-1 million, 4=100,000-500,000, 5=<100,000, and their scoring of flight altitude where scores 1 and 2 were based on

median flight heights on a non-linear scale but scores 3 to 5 were based on 90th percentile flight heights on that scale.

One of the seabird species that appears most vulnerable to collision mortality at offshore wind farms is the northern gannet *Morus bassanus* (hereafter gannet) (Furness et al., 2013). The impact of collision mortality on gannet populations has been one of the primary concerns of recent planning applications for offshore wind farms. Band model calculations estimate a cumulative total of 2,561 gannets per year may be killed by collisions at constructed and consented offshore wind farms in the United Kingdom sector of the North Sea (MacArthur Green 2018). In relation to the Habitat Regulations Assessment (HRA) component of the planning application for Hornsea Two offshore wind farm, Natural England (2015) were unable to conclude beyond all reasonable scientific doubt that the estimated cumulative collision total for offshore wind farms would not have an adverse effect on the integrity of the Flamborough and Filey Coast proposed Special Protection Area (FFC pSPA) gannet population. In relation to East Anglia THREE offshore wind farm, The Planning Inspectorate (2017) stated “two key HRA matters were the focus of the Examination: The effect of the proposed development in combination with other offshore wind farms on the kittiwake and gannet features of the FFC pSPA”. Therefore, estimated collision mortality of gannets has the potential to stop the considerable further development of offshore wind farms planned for the North Sea (The Crown Estate, 2018).

Garthe and Hüppop (2004) assigned a nocturnal flight activity score of two for gannets, based on evidence from Garthe et al. (1999, 2000, 2003) and Hamer et al. (2000), and this was converted to 25% of the daytime level by Band (2012). During mid-summer, the correction for nocturnal flight activity makes only a small difference to estimated numbers of collisions, since the night is short in mid-summer (Fig. 1). However, in winter the effect is larger: because the night is about twice as long as day during winter, the Band (2012) model estimates an additional 0.5 collisions at night for each collision during the day for an offshore wind farm located in the southern North Sea. Most offshore wind farms in Europe are in the southern North Sea. Gannet numbers in that region are low in summer and peak strongly during November (Stone et al., 1995, Furness et al., 2018), so the influence of nocturnal correction is likely to be close to the 0.5 nocturnal collisions per daytime collision. This means that an evidence-based correction for this parameter would be important in improving confidence in

the estimated cumulative impact of collisions at offshore wind farms on gannet populations, especially where the cumulative total is close to a level that could result in consenting risk for further offshore wind farm developments.

Garthe and Hüppop (2004) did not provide an explicit definition of day and night. Collision risk modelling using the Band model defines day as sunrise to sunset and night as sunset to sunrise, with the estimation of the times of sunrise and sunset derived from Forsythe et al. (1995). However, that definition of night contrasts with the official concept of 'twilight' and 'night'. 'Civil twilight' is defined as from sunset to the sun falling 6° below the horizon and in the morning from when the sun reaches 6° below the horizon until sunrise. 'Nautical twilight' is defined as the sun being between 6° and 12° below the horizon. 'Astronomical twilight' is defined as the sun being between 12° and 18° below the horizon, and 'night' is from then until the sun has risen back to 18° below the horizon. In the regions where gannets overwinter, the transition through twilight can be rapid. However, in summer, there may be no official 'night' at all, because astronomical twilight persists if the sun never falls more than 18° below the horizon (Fig. 1). This suggests that a more subtle definition of 'day' and 'night' is required than that used in Band (2012) to take account of the considerable variation in light levels between sunset and sunrise in summer, and especially at higher latitudes. Since gannets are visual predators (Garthe et al., 2000, 2003, Lewis et al. 2002), it is likely that flight activity is determined by the minimum light levels to allow foraging, commuting or migrating. Cleasby et al. (2015a) noted that gannet dives tend to be shallower close to sunrise and sunset, which supports the argument that diving at twilight is limited by the birds' ability to see their prey.

There are now many data sets showing flight activity levels of gannets at different times of day, both for breeding birds and for birds during the migration period and in winter. In this paper we assess the available evidence in order to provide evidence-based corrections for nocturnal flight activity of gannets for use in Band model collision assessments. This will give more accurate results than estimates based on the conversion of scores assigned by Garthe and Hüppop (2004). Here we consider data from throughout the range of the gannet. However, we focus on deriving appropriate corrections for use in examining impacts on gannets in the North Sea, the region with by far the largest number of constructed and proposed offshore wind farms (The Crown Estate, 2018).

2. Methods

We carried out a literature search, focused on Web of Knowledge and Google Scholar but also searching 'grey literature' (such as consultant reports and SNCB guidance documents) to find data on daytime and nocturnal flight activity of gannets. GLS logger data (from Garthe et al., 2012) were used in order to identify variation in flight behaviour according to the time of day. We considered activity data divided into 'day', 'civil twilight', 'nautical twilight', 'astronomical twilight', and 'night' (Fig. 1). We used Time and Date (2018) to extract timings of sunrise, sunset, civil, nautical, astronomical twilight and night appropriate for the location and date of each study.

We considered data derived from tags deployments: a) data from breeding gannets incorporated into Garthe and Hüppop (2004), b) data from breeding gannets collected since Garthe and Hüppop (2004), c) geolocator (GLS) data from gannets during the non-breeding season, d) data from tags on immature gannets (Jeglinski et al. unpublished data). Flight activity is frequently referred to as the percentage of each hour spent in flight. Several different types of tag have been used to infer at sea behaviours of seabirds. Travel speed of birds at sea derived from GPS tracking can be assigned to resting on the sea or to flying if there is a clearly bimodal distribution of travel speeds, with the faster mode representing flight (Gremillet et al., 2004). Few studies have used accelerometer data from tags, but these can aid interpretation of behaviour of birds (Warwick-Evans et al., 2015). Geolocator tags that have a salt-water switch provide accurate data for gannets because birds are either in the water (switch on) or flying (switch off), as it can be assumed that gannets are not on land during the nonbreeding season when away from the colony (Garthe et al., 2012). Some loggers record diving activity but not flight activity. Since gannets only dive from the air, and not from the sea surface, diving activity implies flight activity.

Details of tag types deployed in different studies and numbers of data sets obtained are summarised in Table 1. Garthe et al. (1999) deployed GPS loggers on adult gannets at Hermaness, Shetland. Their loggers provided data on feeding events and on flight activity throughout the 24-hour period, but the study was limited to a sample of just three individuals tracked for a few days in mid-July 1997. Garthe et al. (2000) deployed time-depth loggers on adult gannets at Funk Island, Canada. Hamer et al. (2000) deployed satellite PTTs on chick-rearing gannets at the Bass Rock, Scotland. Garthe et al. (2003) deployed loggers on chick-

rearing adult gannets at Funk Island, Canada recording diving activity and flight activity. Hamer et al. (2007) presented data from satellite tracking or GPS loggers over three breeding seasons for a total of 53 gannets breeding on the Bass Rock. RSPB deployed satellite PTTs and GPS tags on gannets breeding at Bempton during three breeding seasons (2010, 2011 and 2012), obtaining tracks of chick-rearing birds and some tracks of post-breeding dispersal and migration. Garthe et al. (2014) reported on diving activity of breeding birds from Bonaventure, Canada. Warwick-Evans et al. (2015) presented data on the diurnal pattern of plunge dives by gannets breeding at Alderney, Channel Islands. Garthe et al. (2017) reported on plunge diving activity of breeding birds from Helgoland, Germany. Garthe et al. (2012) deployed geolocator loggers on breeding adult gannets on the Bass Rock in 2002, 2003, and 2008, and presented data on flight and resting behaviour of those birds.

Although we were able to access published data on flight activity of adult gannets, no data on flight activity of immature gannets have been published. We therefore include new data on immature gannets. Jeglinski (unpublished data) deployed 7 GPS GSM tags (Pathtrack Ltd. Leeds, UK) on 2-3 year old immature gannets on the Bass Rock between the 3rd and the 11th of July 2016. These tags were equipped with a dynamic algorithm that adjusts the GPS fix rate to the battery voltage, and the GPS fix rate was programmed to 5 minute intervals but in reality GPS fixes were taken every 10 ± 5.4 minutes. Based on the location and timestamp of each position, the data were categorized into four categories (dawn, day, dusk, night) using the function `crepuscule` (R package `maptools`). The function uses algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) to implement flexibility for various formal definitions of times of dawn and dusk. The definition of dawn and dusk was based on a solar angle of $<6^\circ$ below the horizon so represents civil twilight. The speed between successive GPS locations was calculated for each individual and each period. Data were divided into two categories based on the thresholds defined by Bennison et al. (2017) and Wakefield et al. (2013): <3.5 km/hr (likely corresponds to resting e.g. drifting on the sea surface), >3.5 km/hr which may indicate some flight activity as this speed is unlikely to occur due to drift alone, although erroneous high speeds can occasionally occur as a result of inaccuracies in GPS logger location estimates (S. Garthe unpubl. data). We overlay the GPS locations at night with an ocean shapefile based on ocean coastlines at a scale of 10 m (Natural Earth, 2017) to identify if immatures spend the night at sea or on land. All locations

were positioned at sea, so we concluded that immatures do not sleep on land, which is a prerequisite for assigning behaviours as either flying or resting on the sea.

Although differences in methodology among studies might make comparisons of activity budgets between studies difficult, in this paper we only make comparisons within studies, comparing between periods of the day, and so the methodology used in defining flight activity is identical between the relevant periods of the day that we compare.

3. Results

3.1 Breeding adults

Garthe et al. (1999, 2000, 2003, 2014), Hamer et al. (2000, 2007), and Warwick-Evans et al. (2015, 2017) reported that breeding gannet flight activity was negligible during nautical twilight, astronomical twilight and night, and was much lower during civil twilight than during the day. This was also inferred by Langston et al. (2013). The numerous studies of breeding gannets at different colonies and deploying a range of different types of tag show consistent results. Flight (Fig. 2a-e) and diving activity (Fig. 3a-c) of gannets occurred throughout the daylight period, sometimes with a slight tendency to peak just after sunrise and to a lesser extent just before sunset. Flight and diving activity were lower immediately after sunset and immediately before sunrise than during the day, and fell to negligible levels shortly after sunset. Flight activity remained at negligible levels through the night until shortly before sunrise (Fig. 2a-e). When averaged over the period from sunset to sunrise, flight activity of breeding adults averaged 7.1% of the daytime level across six studies, while diving by breeding adults averaged 2.9% of the daytime level across seven studies (Table 1).

3.2 Immatures

Tracked immature gannets moved at an average speed of 1.4 ± 1.21 (SE) km/h during nautical and astronomical twilight and night. Based on the threshold metric, 95.3% of the time periods were defined as birds resting on the water (Electronic Supplement Table S1). During dawn the average speed was 3.67 ± 6.44 km/h, which is higher than at night, so suggests some flight activity. During dusk the average speed was 8.87 ± 14.81 km/h, also higher than at night and suggesting some flight activity. Based on the threshold metric, on average 83.3% and 65.8% of dawn and dusk periods were identified as birds resting on the water. With a typical flight

speed of 25 km/hr (e.g. Hamer et al., 2000), birds would have to spend less than 25% of a period in flight even during the few periods when flight appears likely, in order to result in a mean speed of movement of only 4 to 5 km/hr, which was the average maximum speed recorded across the sample of birds during night in the few intervals when some flight activity was indicated (Electronic Supplement Table S2). During the day, 61.7% of time intervals were classified as birds resting on the sea surface. However, during the day, immatures moved with an average speed of 11.48 ± 17.14 km/hr, reaching maximum speeds between 55 and 87 km/hr.

Even though the dominant activity during night was resting, all birds apparently spend a very small proportion of the night in flight. The data show that immature flight activity, based on flight speed, was higher during civil twilight than at night, with birds generally flying faster (and spending almost double the proportion of time periods during which there seemed to be some flight activity) during dusk than during dawn. Overall, the data show low flight activity by immatures between sunset and sunrise, though possibly slightly more than seen among breeding adults.

3.3 Adults in the non-breeding season

Flight activity of adult gannets during the non-breeding season between sunset and sunrise averaged 2.5% of daytime level during autumn and 1.9% of daytime level during winter (Garthe et al., 2012). Data for the subset of birds migrating through the North Sea in autumn, which may be the most appropriate in relation to collision risk at North Sea offshore wind farms, are presented in Figure 2d. During peak autumn migration (mid-late October) adult gannets from the Bass Rock that were going to remain in the North Sea or Channel overwinter spent on average 31.9% of daylight time in flight, 2% of civil and nautical twilight combined in flight and 0% of astronomical twilight and night time in flight. Considering the nocturnal period (sunset to sunrise) flight activity of adult gannets in the North Sea that remained in the area overwinter averaged 1% of the daytime level, whereas flight activity of adult gannets that migrated to winter off southern Europe or west Africa averaged 3.8% of the daytime level (Table 1).

Data for flight activity during winter of birds remaining in the southern North Sea during winter are presented in Figure 2e. In winter (December), birds spent hardly any of the night

or astronomical twilight in flight, with a mean of 0.2% of the night spent flying. Garthe et al. (2012) showed that during daylight hours, birds spent more time flying in autumn than in winter, and birds that were migrating to West Africa spent more time flying during the day (40% of daylight hours) than birds that wintered in UK waters (30% of daylight hours flying). In winter, birds spent on average 26% of daylight hours in flight (Garthe et al., 2012). However, birds wintering in the southern North Sea flew more than birds wintering in west Africa, so that the daytime baseline level of flight activity against which nocturnal activity is compared needs to be considered on a regional basis to ensure a like-for-like comparison. Birds in the southern North Sea in December flew 31% of daylight hours. By comparison, they flew 4.5% of civil twilight and nautical twilight periods, and 0.2% of astronomical twilight and night periods. Flight activity between sunset and sunrise averaged 0.75% of the time, compared with 31% of the time between sunrise and sunset. Flight between sunset and sunrise therefore averaged 2.4% of the rate during the day (Table 1).

4. Discussion

Multiple studies of breeding gannets in multiple years at colonies in Scotland, Germany, Canada and the Channel Islands, and one of immature gannets, all show extremely low levels of flight activity of gannets at night, and no plunge diving at night (Table 1). Data from birds in the non-breeding season show flight activity between sunset and sunrise is consistently around 1% to 4% of the amount recorded during daytime. Data from breeding adults show flight activity between sunset and sunrise averaging 7% of the daytime level, with diving activity between sunset and sunrise averaging 3% of the daytime level (Table 1). Higher nocturnal flight activity of breeding adults than of adults during the non-breeding season could possibly reflect high energy demands of breeding, forcing birds to extend foraging effort, but may simply result from the fact that almost all nocturnal flight activity occurs during civil twilight. In summer, civil twilight lasts longer than in winter (Fig. 1), and there may be no astronomical twilight or night. In winter, night represents a much greater proportion of the period from sunset to sunrise (Fig. 1), so lack of flight activity at night reduces the average level of flight activity between sunset and sunrise during winter compared to summer.

The logger data from non-breeding adult gannets are robust as they are from a large sample size over several winters (Garthe et al., 2012), and can be disaggregated by region and by migration extent of individuals. The low level of flight activity at night is consistent with the understanding of gannet natural history; as visual hunters gannets will not be able to locate fish on which to plunge-dive during hours of darkness (Lewis et al. 2002, Cleasby et al. 2015a), and in the non-breeding season will not need to fly at night to return to nest sites. Gannet migrations are very slow compared to migrations of other seabird species (Garthe et al., 2012; Fifield et al., 2014) and so birds are not under any pressures to migrate during the night.

It is unclear whether differences in estimates of nocturnal flight activity among studies of breeding adults represent differences in behaviour of birds from different colonies or simply reflect chance variation. The largest estimates of the amount of nocturnal flight activity by breeding adults tended to come from the studies based on the smallest sample sizes; a weighted average based on the number of birds in each study would reduce this estimate by about 50%. However, it is also possible that ecological conditions affect amount of flight activity by breeding gannets. The highest estimate of flight activity between sunset and sunrise (20.9% of the daytime level) was from Garthe et al. (1999) who studied just three birds at a colony in Shetland. At that latitude in summer there is a long period of civil twilight, and no astronomical twilight or night. Birds at higher latitude colonies (such as Shetland) might show relatively more nocturnal flight because civil twilight represents a greater part of the period from sunset to sunrise than further south.

Diving activity (and therefore foraging rather than commuting flight) was even less frequent between sunset and sunrise than flight activity. Given that collision risk is higher when gannets are foraging rather than when they are commuting (Cleasby et al., 2015b), the low amount of foraging flight during the twilight period will further reduce collision risk at that time of day compared to flight during the day. This suggests that a case could also be made for using a lower flight height distribution for the few birds still flying during twilight compared with that used for gannets flying during the day.

Gannet flight activity differs considerably between daytime, civil twilight, and darker periods (nautical twilight, astronomical twilight and night). Thus there would be merit in developing a more nuanced Band model taking account of the activity patterns in these different periods. This, additionally, would account for the very different durations of twilight and night at

different times of year. However, in the short term, predictions from Band modelling could be improved by adopting the evidence-based values for flight activity during the nocturnal period (i.e. from sunset to sunrise) in the current Band model.

Based on the average percentage of daytime flight activity that was observed between sunset and sunrise, we recommend that precautionary values of the nocturnal activity factor used with the Band model for estimating collisions should be 8% during the breeding period and 3% during the nonbreeding period. This would not require the Band model to be altered to add separate calculations for twilight periods, although that might be a longer term objective. These values are strongly founded on evidence, and are more appropriate than the 25% value currently suggested by Band (2012) which was not evidence-based. Furthermore, we consider that these evidence-based estimates remain precautionary because they use the unweighted average across studies, and a weighted average accounting for sample sizes would reduce the estimate for breeding birds further. Tracking data exist for several other seabird species. However, most data sets have not been published in a form that allows nocturnal flight activity to be seen. Given that the evidence-based estimates for gannet represent a large reduction from the value employed by Band (2012), there would be merit in analysing nocturnal flight activity of species such as kittiwake *Rissa tridactyla*, great black-backed gull *Larus marinus* and lesser black-backed gull *L. fuscus*. Evidence-based estimates for those species would also help to reduce uncertainty in environmental impact assessments for offshore wind farms.

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Table 1. Summary of flight and plunge-diving activity between sunset and sunrise in relation to daytime levels

Reference	Season	Colony	Number of tags and tag type	Hours of data on foraging trips	Flight activity from sunset to sunrise as % of flight activity during day	Number of plunge dives recorded	% of plunge dives occurring between sunset and sunrise
Garthe et al., 1999	Breeding	Hermaness	3 stomach temperature	215	(20.9%)	32	(0%)
Garthe et al., 2000	Breeding	Funk Island	11 depth & wing-beat		-	336	4.3%
Hamer et al., 2000	Breeding	Bass Rock	17 Argos satellite PTTs	>2000	0%	-	0
Garthe et al., 2003	Breeding	Funk Island	16 depth & temperature	330	6%	315	0.5%
Hamer et al., 2007	Breeding	Bass Rock	53 Argos PTTs, or GPS tags	>5000	0%	-	-
Langston et al., 2013	Breeding	Bempton	42 Argos satellite PTTs	-	0%	-	-
Garthe et al., 2014	Breeding	Bonaventure	5-7 GPS & altimeter	-	-	731	15%
Warwick-Evans et al., 2015	Breeding	Alderney	9 GPS & accelerometer	678	-	1236	0%
Warwick-Evans et al., 2017	Breeding	Alderney	9 GPS & accelerometer	678	15.7%	-	-
Garthe et al., 2017	Breeding	Helgoland	14 GPS & depth	-	-	2557	0.7%
Garthe et al., 2012	Autumn	North Sea	59 geolocator & temperature	-	2.5%	-	-
Garthe et al., 2012	Winter	North Sea to Africa	50 geolocator & temperature	-	1.9%	-	-
This analysis	Autumn	Remaining in North Sea	4 geolocator & temperature	35 days	1%	-	-
This analysis	Autumn	Migrating to Africa	8 geolocator & temperature	71 days	3.8%	-	-
This analysis	Breeding	Bass Rock, immatures	7 geolocator & temperature	4 days	Very low	-	-
This analysis	Winter	Birds in North Sea	4 geolocator & temperature	-	2.4%	-	-

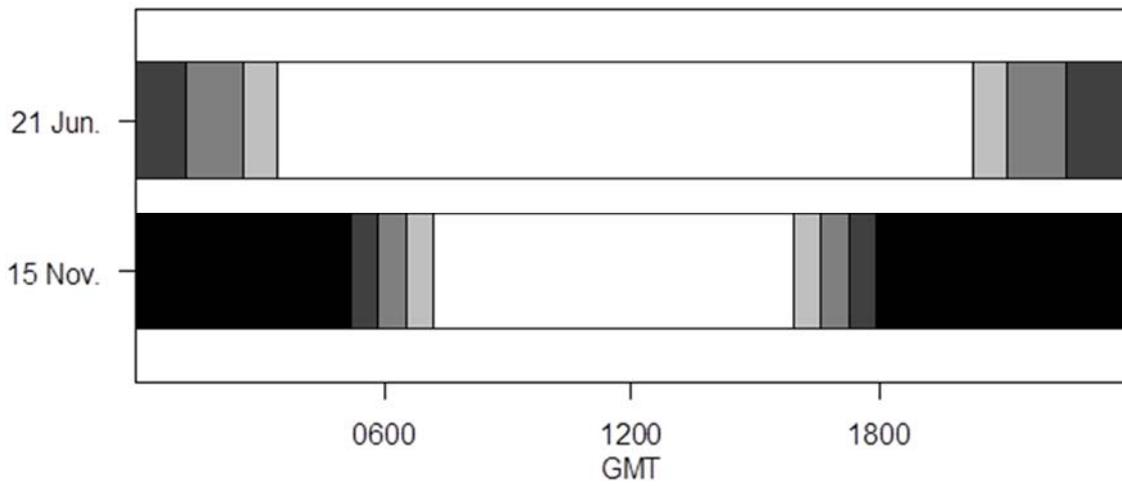


Fig. 1. Illustration of the differences in duration of night (black), astronomical twilight (dark grey), nautical twilight (medium grey), civil twilight (light grey), and day (white) at midsummer (21 June) and during peak migration of gannets through the southern North Sea (November) at 52°30'N 2°30'E, a typical location for a southern North Sea offshore wind farm. Times in GMT.

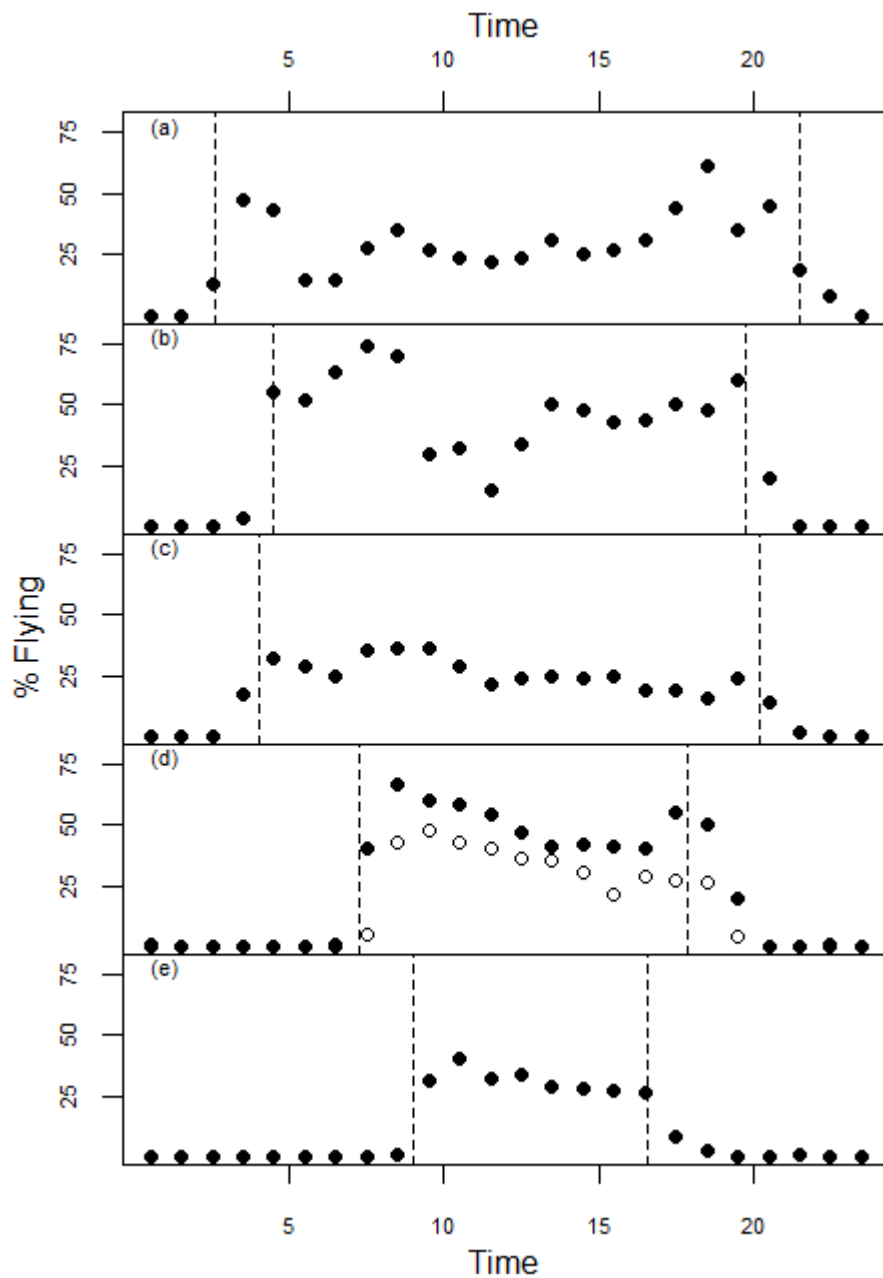


Fig. 2. Flight activity of gannets in relation to hour of the day a) in mid-July 1997 at Hermaness, Shetland (Garthe et al., 1999); b) of chick-rearing gannets from Funk Island, Canada (Garthe et al., 2003); c) of breeding adult gannets at Alderney, Channel Islands in June 2013 (Warwick-Evans et al., 2017); d) in autumn migration (mid-late October) of adult gannets that overwinter in the North Sea (open symbols) or were migrating to overwinter in west Africa (solid symbols) (Garthe et al., 2012); e) in December by adult gannets from Bass Rock that

remained in the southern North Sea through winter (Garthe et al., 2012). Dashed lines show times of sunrise and sunset.

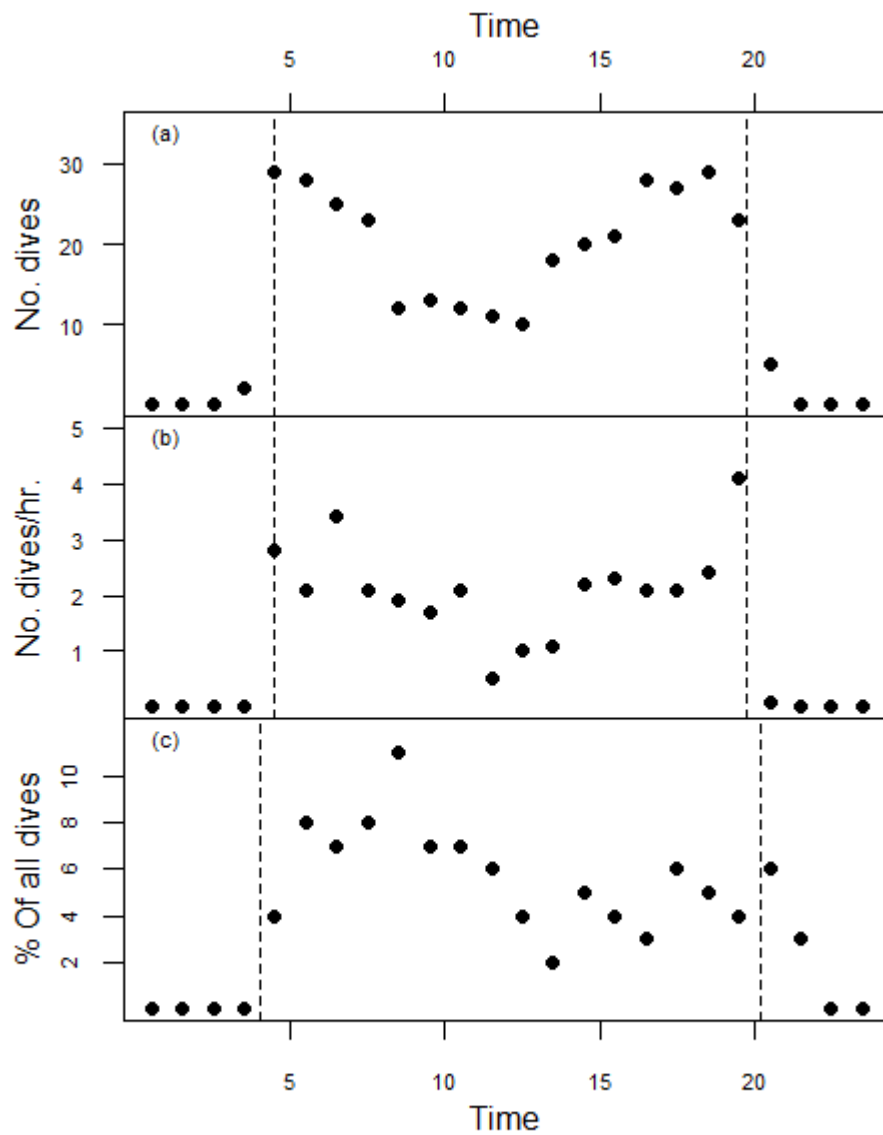


Fig. 3. Diving activity of chick-rearing gannets from a) Funk Island, Canada at different times of day (Garthe et al. (2000)). b) Funk Island, Canada at different times of day (Garthe et al. (2003)). c) Bonaventure Island, Canada at different times of day (Garthe et al. (2014)). Dashed lines show times of sunrise and sunset.

Electronic Supplement. Table S1: Summary of time budgets of seven immature gannets based on categories: speed <3.5 km/h defined as birds resting on the water, speed >3.5 km/h defined as birds possibly spending part of that period in flight

Tag	Period	Periods when speed indicates birds were resting on sea surface (%)	Periods where some flight may have occurred (%)
14904	Day	68.4	31.6
14904	Dusk	68.2	31.8
14904	Night	95.7	4.3
14904	Dawn	84.1	15.9
14905	Day	59.6	40.4
14905	Dusk	63.4	36.6
14905	Night	93.0	7.0
14905	Dawn	80.6	19.4
14907	Day	38.1	61.9
14907	Dusk	58.3	41.7
14907	Night	89.4	10.6
14907	Dawn	81.0	19.0
14908	Day	66.6	33.4
14908	Dusk	79.3	20.7
14908	Night	97.5	2.5
14908	Dawn	77.9	12.1
14909	Day	65.5	34.5
14909	Dusk	60.5	39.5
14909	Night	98.1	1.9
14909	Dawn	89.0	11.0
14910	Day	73.9	26.1
14910	Dusk	65.0	35.0
14910	Night	99.1	0.9
14910	Dawn	98.8	1.2
14912	Day	60.0	40.0
14912	Dusk	66.2	33.8
14912	Night	94.2	5.8
14912	Dawn	71.5	28.5

Electronic Supplement. Table S2. Summary statistics of GPS sampling interval, distance between subsequent locations and speed for the seven immature birds tracked in July 2016.

Tag	period of day	time between locations (mean \pm sd, min)	distance (mean \pm sd, km)	speed (mean \pm sd, km/h)	speed (max, km/h)
14904	night	6.31 \pm 2.48	0.16 \pm 0.20	0.92 \pm 1.25	10.23
	dawn	7.60 \pm 2.56	0.53 \pm 0.79	5.28 \pm 9.72	35.95
	day	7.08 \pm 2.70	1.31 \pm 3.50	9.16 \pm 16.56	77.27
	dusk	6.71 \pm 2.41	0.93 \pm 1.54	9.62 \pm 15.64	43.87
14905	night	10.13 \pm 3.72	0.26 \pm 0.39	1.79 \pm 2.74	26.33
	dawn	10.65 \pm 4.95	0.74 \pm 1.67	4.32 \pm 10.06	36.80
	day	11.06 \pm 4.80	2.23 \pm 3.5	13.22 \pm 19.18	87.07
	dusk	9.68 \pm 3.68	1.30 \pm 1.99	8.72 \pm 12.72	36.98
14907	night	11.91 \pm 4.66	0.39 \pm 0.30	1.95 \pm 1.16	6.94
	dawn	10.66 \pm 4.97	0.37 \pm 0.29	2.41 \pm 1.34	5.25
	day	12.86 \pm 10.72	3.26 \pm 5.21	15.47 \pm 17.88	63.69
	dusk	10.53 \pm 5.10	1.17 \pm 2.78	5.37 \pm 10.90	59.17
14908	night	7.11 \pm 6.44	0.11 \pm 0.08	1.22 \pm 0.80	5.73
	dawn	6.24 \pm 2.64	0.61 \pm 1.12	6.25 \pm 11.64	45.49
	day	7.07 \pm 11.08	1.04 \pm 1.67	11.08 \pm 17.18	73.50
	dusk	6.25 \pm 4.12	0.66 \pm 1.51	8.02 \pm 15.61	62.37
14909	night	13.11 \pm 2.75	0.18 \pm 0.10	0.87 \pm 0.54	2.44
	dawn	13.19 \pm 2.99	0.80 \pm 2.22	3.44 \pm 8.83	42.94
	day	12.39 \pm 4.36	2.04 \pm 3.15	10.51 \pm 15.91	55.57
	dusk	13.27 \pm 2.66	2.58 \pm 3.98	12.99 \pm 19.46	56.21
14910	night	9.76 \pm 4.00	0.26 \pm 0.22	1.28 \pm 0.89	3.27
	dawn	9.91 \pm 3.87	0.22 \pm 0.09	1.59 \pm 0.83	2.97
	day	10.94 \pm 3.82	1.44 \pm 3.00	7.47 \pm 14.66	80.45
	dusk	9.88 \pm 4.05	1.48 \pm 1.98	10.52 \pm 14.81	44.16
14912	night	11.77 \pm 2.74	0.26 \pm 0.22	1.40 \pm 1.11	5.37
	dawn	11.52 \pm 2.6	0.46 \pm 0.50	2.43 \pm 2.64	14.79
	day	11.68 \pm 3.51	2.53 \pm 3.67	13.48 \pm 18.57	77.23
	dusk	11.12 \pm 2.77	1.38 \pm 3.34	6.88 \pm 14.53	58.60