Gulls of a feather do not sleep whenever—circadian rhythm of activity of black-headed gulls *Chroicocephalus ridibundus* during the incubation period

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Received: 13 January 2021 / Revised: 23 April 2021 / Accepted: 5 May 2021 / Published online: 29 May 2021
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Abstract

Many vertebrates exhibit a diel activity, steered by light–dark cycle. However, some colonial waterbirds, in that several species of gulls, are active not only in day hours but also at night. In this study, we aimed to investigate 24 h cycle of black-headed gulls (BHG) *Chroicocephalus ridibundus* activity with focus on sleep behaviour. We expected that 24 h patterns of activity differ between colonies located in various habitats, and within a colony between nests located in the centre vs at the edge. We studied behaviour based on 9600 of 30 s videos from camera-traps taken in six colonies and data from 10 GPS-tracked individuals from one colony recorded during incubation. BHGs stayed active on average during 48.1% of a night, mainly spent on passive and active nest defence, and on nest maintenance. BHGs spent similar time on these activities in day hours. Individuals breeding in the colony centre slept at night longer than those at its edge. BHGs stayed active during on average 76.5% of daytime. In two urban colonies with the highest nest densities and highest level of light pollution birds slept less during the day than in other studied colonies (three rural and one urban) characterized by lower densities and light intensity after sunset near the colony. Knowledge of nocturnal behaviour is crucial to comprehend 24 h activity patterns of an organism, especially to understand flexibility of behaviour crucial for restoration, like sleep.

Keywords Nocturnal activity · Time-activity budget · Circadian rhythm · Colonial waterbird · Sleeping behaviour

Communicated by S. Bouwhuis.

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Zusammenfassung

Möwen schlafen bei Weitem nicht zu selben Zeiten—circadianer Aktivitätsrhythmus bei Lachmöwen während der Brutzeit

Viele Wirbeltiere weisen eine Tagesaktivität auf, die durch den Helldunkel-Zyklus gesteuert wird. Einige koloniebildenden Wasservögel, darunter wenige Möwenarten, sind jedoch nicht nur tagsüber, sondern auch nachts aktiv. Ziel dieser Studie war es, den 24-Stunden-Aktivitätszyklus von Lachmöwen *Chroicocephalus ridibundus* (engl. *Black-headed Gulls*, BHG) mit Schwerpunkt auf dem Schlafverhalten zu untersuchen. Wir erwarteten, dass sich das 24-Stunden-Aktivitätsmuster zwischen Kolonien in verschiedenen Habitaten und innerhalb einer Kolonie zwischen Nestern im Zentrum und denen am Rand unterscheiden. Wir untersuchten das Verhalten anhand von 9.600 30-Sekunden-Videos von Kamerafallen, die in sechs Kolonien aufgestellt wurden, und anhand von Daten von zehn mit GPS-Loggern versehenen Individuen aus einer Kolonie, die während der Brutzeit aufzeichneten. BHGs blieben durchschnittlich 48,1% einer Nacht aktiv und verbrachten diese Zeit hauptsächlich mit passiver und aktiver Nestverteidigung sowie Nestpflege. BHGs verbrachten tagsüber ähnlich viel Zeit mit diesen Aktivitäten. Individuen, die im Koloniezentrum brüteten, schliefen nachts länger als am Rande brütende Individuen. BHGs blieben durchschnittlich 76,5% der Tageszeit aktiv. In den Kolonien mit den niedrigsten Nestdichten schliefen die Vögel tagsüber mehr als in Kolonien mit den höchsten Nestdichten. Die Länge des Schlafes während des Tages wurde durch die Lichtintensität nach Sonnenuntergang in der Nähe der Kolonie beeinflusst, und BHGs in städtischen Kolonien schliefen weniger als solche in ländlichen Kolonien. Die Kenntnis über das nächtliche Verhalten ist entscheidend für das Verständnis des 24-Stunden-Aktivitätsmuster eines Organismus, insbesondere wenn es um für die Erholung wichtige, flexible Verhaltensweisen wie den Schlaf geht.

Introduction

Gulls, as many other groups of birds, are commonly considered active only during the day (Burger 1988; Yorio et al. 2005; Hayes and Hayward 2020). However, some colonial waterbirds including at least 20 species of gulls have been reported to be active also at night (Burger and Staine 1993; McNeil et al. 1992, 1993). Knowledge on nocturnal activity of gulls is poor and fragmentary, and considers mainly night foraging or feeding chicks, and copulations at night (e.g., Leck 1971; Underhill 1987; Tarburton 1991; Yorio et al. 2005), but not the entire spectrum of their activities at night. Among gulls, probably only the swallow-tailed gull *Creagrurus furcatus* feeds exclusively at night (Harris 1970). Other gull species do it irregularly, and rather in favourable environmental conditions, as moonlight in cloudless nights or artificial light from trawlers, lighthouses and airports. It has been shown that insects lured by artificial lights are preyed by grey-headed gulls *Chroicocephalus cirrocephalus* (Underhill 1987) and silver gulls *Chroicocephalus novaehollandiae* (Tarburton 1991). Herring gull *Larus argentatus* and slaty-backed gull *Larus schistisagus* have been reported to hunt in moonlit nights for Leach's storm-petrels *Oceanodroma leucorhoa* (Harris 1974; Pierotti and Annett 1987, 1990; Tarburton 1991; Watanuki 1986), and western gulls *Larus occidentalis* for Cassin's auklets *Ptychoramphus aleuticus* (Nelson 1989). Ring-billed gull *Larus delawarensis* and red-legged kittiwake *Rissa brevirostris* in moonlight nights hunt for fish coming to the water surface (Leck 1971; Fetterolf 1979; Hunt et al. 1981a, b). Gray gull *Leucophaeus modestus* (Underhill 1987) and Pallas's gull *Ichthyophaga*

ichthyaetus (Cramp and Simmons 1983) not only forage at night, but also feed chicks. Regular studies of other aspects of nocturnal activities in gulls, e.g. interactions with neighbours, synchronizing timing of sleep with activities of the closest neighbours in a colony (so-called collective waves of sleep—Beauchamp 2011; Evans et al. 2018), or full time budget, are rare.

The aim of our study was to investigate 24 h pattern of activity of the black-headed gull *Chroicocephalus ridibundus* (hereafter BHG) during the period of incubation with special emphasis on nocturnal activity. In a pair, both male and female incubate eggs, swopping regularly at the nest (Cramp and Simmons 1983). During 3.5 weeks of long incubation (Harrison 1975), both partners actively defend their nesting territory against BHGs and other species breeding in their colony (Bukacińska and Bukaciński 1994; Indykiewicz and Minias 2019). In case of danger from predators, the pair jointly defend the colony, but often leave it temporarily (Indykiewicz 2015). During incubation, they forage mainly near the colony, depending on the colony size and environment (Jakubas et al. 2020). Some authors suggest exclusively diurnal activity of this species (Chandler 1983; Wikelski et al. 2006; Evans et al. 2018). However, one may expect that BHG is also active at night, as other gulls (Arcos and Oro 2002; Leopold et al. 2010). Here, we focused on sleep behaviour because severe sleep deprivation can reduce cognitive and physical performance in vertebrates (Rechtschaffen and Bergmann 2002; Shaw et al. 2002; Huber et al. 2004; Rattenborg et al. 2004; Snyder et al. 2013; but see Rattenborg 2017). Thus, one may expect that sleep deficits may

require compensatory adjustments at the expense of other activities (Fuchs et al. 2006).

In this study, we investigated whether 24 h pattern of sleep behaviour in the studied colonial represents a flexible response to social or environmental factors (Lima 2005). We formulated the following hypotheses:

- (1) individuals that sleep short at night compensate this nocturnal sleep deficiency during the day to secure restoration of organism and unbiased cognitive and physical performance (Rattenborg et al. 2004, 2009; Fuchs et al. 2006; Németh 2009; Covino and Cooney 2015);
- (2) in the colonies with the highest nest densities, BHGs spend more time on defending nesting territories, nests and eggs, and in a consequence, they spend less time on other activities, including sleep, compared to individuals breeding in colonies with low densities of breeding pairs (Bukacińska and Bukaciński 1993; Besnard et al. 2006; Druzyaka et al. 2015; Indykiewicz and Minias 2019);
- (3) in the colonies affected by light pollution at night, especially those located in urban areas, BHGs spend less time on nocturnal vigilance and sleep more compared to those in the colonies in rural areas less affected by this factor (Raap et al. 2017; Kempenaers et al. 2010; Steinmeyer et al. 2010; Russ et al. 2015);
- (4) birds breeding at peripheries of colonies spend less time on sleep, both at day and night, compared to pairs breeding in the core centre of a colony, in response to stress of danger from potential predators (Velando and Freire 2001; Lima 2005; Minias 2014).

Materials and methods

Study area

We studied BHGs during the incubation period in six breeding colonies in N Poland in 2016–2019. All colonies were situated on islands in the lakes or rivers in farmland or urban areas. The colonies differed in the number and density of breeding pairs, the structure and diversity of vegetation covering an island, and the structure of surface around a water body. Three urban colonies (in Bydgoszcz town) were located 0.9–6.1 km apart. Two of them (BYD-SP and BYD-PR) were surrounded by strongly developed areas, with factories, service buildings and railway. The third colony (BYD-LP) was situated in the recreational area near the northern border of the town, about 5 km away of its core centre. Three rural colonies were surrounded mostly by arable fields, meadows and forests (Fig. SM1, Table SM1, Supplementary Materials).

Recording behaviour of black-headed gulls

In all six studied colonies, behaviour of BHGs was recorded automatically with camera traps TV624M (BUSHNELL, USA) with No-Glow LEDs. They were installed at least 0.9 m away of the focal nest. To entirely eliminate the risk of nest abandonment by BHG, the camera traps in cryptic colours were additionally masked using vegetation.

Two to five camera traps at a time were set up in a colony, depending on its size and surface relief. Camera traps were located in the colony at the distance of a few or few tens of metres from each other in such a way that each of them recorded different 2–3 nests. This prevented simultaneous recording of birds representing the same group (e.g. nesting at the edge or in the centre of the colony). This camera setting eliminated any risk of simultaneous recording of birds from neighbouring groups, and thus avoiding recording the copied behaviour of neighbours, so-called “collective waves of sleep” (Beauchamp 2009, 2011, 2012).

Behaviour of BHG was recorded in all colonies between 21 April and 1 June (mid and late incubation period), during day and night. Because the time of sunrise and sunset changed over this period (sunrise—05:35 and 04:27, sunset—19:57 and 21:03, on 21 April and 1 June, respectively, according to the Central European Time) the length of days and nights also changed. On 21 April, the day length was about 14.5 h and the night was 9.5 h, but on 1 April 16.5 and 7.5 h, respectively.

We selected only the nests with three eggs (the full clutch), and where no more than 14 days had passed since the last eggs had been laid. Such approach eliminated any potentially harmful effect of the person setting the camera traps on abandoning the clutch at the last stage of chick hatching. All camera traps were programmed to record the view according to the same time schedule. In practice, they recorded 30 s of vision and sound in 30 min intervals, during six time intervals (T1–T6), considering natural variation of birds' activity during the day and night. At the first day of recording (21 April), the time intervals were: 5:30–7:00 (T1), 12:00–13:30 (T2), 18:30–20:00 (T3), 21:30–23:00 (T4), 00:00–1:30 (T5) and 3:00–4:30 (T6). In subsequent days, until 1 June, the time periods were adjusted to changing times of sunrise and sunset. In practice, this meant recording three movies in each time interval (T1–T6), thus 18 movies per 24 h, for each nest within the scope of a camera trap. Usually two or three nests were located within the scope of recording by a camera trap, depending on the distance between the nests. Each nest was filmed only over one 24 h period. Each filmed nest was individually marked with a small marker (30×50 mm) with the nest number, and its location was recorded on a map. This procedure ensured that birds from each nest were not filmed in subsequent days of study. Individuals in recorded nests were not individually

marked, because our study was aimed to investigate the time budget of birds remaining in the colony, not to record activities of individuals.

We recorded a total of 11,680 movies. However, for final analysis, we qualified 9697 movies (Table SM2, Supplementary Materials), which recorded behaviour of 534 BHGs in full time schedule, i.e. 18 movies, three in each time interval T1–T6. Excluded movies were characterized by, insufficient quality caused for example by fog, rapid rainfall, camera falling etc.

Analysed types of behaviour

While determining the time budget of BHGs during egg incubation, we focused mainly on behaviour of birds that remained in the nest. We consider neither involvement of each individual in a pair with incubation of eggs nor their behaviour outside the breeding colony, as foraging or rest outside the island, bathing in water, etc.

Based on the collected documentation, we distinguished in BHGs the following types of behaviour:

- sleep (SLE)—the stage in which a bird had eyes closed and was sitting or standing, and laid bill under or on feathers of the back (back sleep), or lowered head and leaned its bill against breast (front sleep). Sporadic opening eyes (blinking) was treated as a natural element of sleep, as described by Amlaner and McFarland (1981) and Amlaner and Ball (1994);
- defence of nest and nesting territory—reaction of birds to appearance of predator, human intruder (gravel pit worker and swimmer/sunbather) or interspecific in a close proximity of the nest; we divided this type of behaviour into two subcategories: 1) active defence (ADE)—when BHG was involved in an aggressive interaction with one or several individuals, or when BHG remaining in the nests stretched its neck towards a neighbour or intruder and usually vocalized, 2) passive defence (PDE)—when the recorded individual stayed in the nest in sitting position with eyes opened, but without any elements of aggressive behaviour or any other activities (e.g. preening, fixing nest material or turning eggs);
- preening (PRE)—this behaviour included mainly cleaning feathers, fixing their structure and arranging them, and combing feathers to remove ectoparasites;
- nest maintenance (NEM)—fixing the structure of a nest and adding building material, usually found near the nest;
- common activities of a pair (COA)—e.g. bowing to greet each other, copulation, mutual grooming, swapping partners on a nest;
- other activities (OTA)—e.g. improving arrangement of eggs or turning them, preparations for flight and leaving

the nest, stretching wing and leg on one side while standing;

The duration of these activities was determined during playing subsequent movies recorded by camera traps. This job was conducted in comfortable conditions by one person (JG).

GPS-tracking

To characterize 24 h pattern of BHGs flights during the incubation period, we used small PinPoint-10 GPS store-on-board loggers (1.3 g; Lotek Wireless Inc.), which recorded time and position. We deployed loggers on one member of a pair in 10 nests from the colony BYD-PR. We captured birds on nests during the second to fourth week of the incubation period using spring traps (ECOTONE) or loops made of nylon strings. We attached the tags to the central back feathers of each bird using two 3–4 mm-wide strips of tape code 4.965 (TESA Tape Inc.) crosswise-applied approximately at the midpoint of the centreline of the body. The logger weight (1.6 g, including attachment) was on average equivalent to 0.69% body mass of the captured individuals.

We set the loggers to collect data at 15 min intervals. After about 48 h from logger deployment, we tried to recapture birds and retrieve the loggers. We deployed 10 loggers and recaptured all birds successfully. In total, we analysed 36 trips from 10 individuals. In that for six individuals, we recorded locations both at the day and night from 10 to 26 May; four remaining individuals showed locations only in diurnal hours. To estimate influence of GPS-logger equipped individuals on their breeding performance, we compared hatching success in nests of equipped individuals ($N=10$) and in control nests with not logger-burdened individuals ($N=151$). We chose control nests with the same clutch size as in the nests of the logger-equipped birds, i.e. containing three eggs. We found that hatching success was similar in the nests with GPS-logger burdened one of the parents (93.3%) and in the control nests (78.8%; chi-squared test of independence, $\chi^2=0.387$, $df=1$, $p=0.534$).

Statistical analyses

Factors affecting relative duration of sleep behaviour

To analyse proportion of time devoted to sleeping behaviour per recording unit, we firstly divided the duration of sleep by the recording time (30 s). As the distribution of the data on sleeping behaviour departed from normal and had bimodal distribution, we used beta regression. Since in beta regression, values should not include 0 and 1 and our data did, we used transformation $x=(x^*(n-1)+0.5)/n$, where n was the

sample size (Smithson and Verkuilen 2006), here the number of all analysed 30 s recordings ($N=9697$).

To analyze factors affecting the relative duration of sleep, we used beta regression mixed model with colony, colony sector (central, peripheral), day/night, and their interactions as factorial predictors and nest identity as a random factor. We considered nests located in the 0–1.5 m wide zone adjacent to the water line (island edge) as peripheral; those located > 1.5 m from the water line as central.

As the observed individuals were not individually marked, we used nest identity, not bird identity as the random factor. As BHGs partners share incubation duties equally (Ytreberg 1956; Beer 1961), we assume that our results are not biased by overrepresentation/underrepresentation of one of the sexes.

We performed beta regression models in *glmmTMB* (Brooks et al. 2017), post hoc estimated marginal means tests in *lsmeans* (Lenth 2016) packages in R software (R Core Team 2019).

Differences in relative duration of each behaviour

To compare relative duration of each type of behaviour between the night and day, and between the colonies, we used *G* test for independence in *rcompanion* package (Fox and Weisberg 2011) in R software. In some analyses, we considered all types of behaviour as 100% of time, in other analyses all types of behaviour excluding sleep were 100%. We applied the second approach because BHGs spent most time on sleeping, which masked the importance of other less frequent behaviours. To compare daily distributions of the relative duration of each type of behaviour between the colonies, we used Anderson–Darling *k* sample test in *kSamples* package in R software (R Core Team 2019). We analysed values averaged for each time interval (T1–T6).

Relationship between sleep duration and various external factors

To investigate relationships between relative sleep duration in each colony with the colony size, colony density and intensity of nocturnal light pollution, we used Pearson correlations. We performed separate analyses for diurnal and nocturnal sleep behaviour. To check whether denser colonies are not located in the areas with higher light pollution levels (e.g. because of closer location to the urbanized areas), we also investigated relationship between the nest density and light pollution.

Flights of GPS-tracked individuals

We analysed the following characteristics of BHGs trips based on geographical positions recorded by the GPS loggers:

- (1) maximum range of flights (km)—the distance from the colony to the distal point reached on each foraging trip;
- (2) total distance covered (km)—the sum of distances between consecutive GPS positions along each individual's track;
- (3) total trip duration (min)—the time between departure and return to the colony.

We defined as a trip flights with at least three positions recorded in a minimum distance of 1 km away of the colony.

To compare the listed characteristic of trips between day and night, we used mixed gamma regression model (maximum range of flights as it departed from the normal distribution) or linear mixed models (total distance covered, total trip duration) with day/night as a factorial predictor and bird identity as a random factor.

We performed mixed gamma regression and linear mixed model in *lme4* and *lmerTest* (Kuznetsova et al. 2017) packages in R software (R Core Team 2019).

In all statistical analyses, we set the alpha level at 0.05. We mapped GPS-tracking data, extracted data from the CORINE model and produced all figures with maps using ArcMap/ArcGIS 10.3.1 (Redlands, CA: Environmental Systems Research Institute).

Results

We found that BHG were active not only at day, but also in late evening and at night. This was documented by recordings from camera traps set near the nests in all studied

Table 1 Effects of studied predictors on the relative length of sleep of black-headed gulls during egg incubation

Predictors	χ^2	df	$\text{Pr}(\chi^2)$	<i>p</i>
Colony	50.526	5	1.082e−09	0.001
Day/night	645.897	1	< 2.2e−16	0.001
Colony sector	15.427	1	8.575e−05	0.001
Colony × day/night	225.444	5	< 2.2e−16	0.001
Colony × colony sector	40.901	5	9.826e−08	0.001
Day/night × colony sector	26.524	1	2.603e−07	0.001
Colony × day/night × colony sector	29.490	5	1.858e−05	0.001

Beta regression mixed model

Table 2 Proportion of time (%) allocated to sleep by black-headed gulls of diurnal, night, diurnal and night combined in 30 s recordings in the studied breeding colonies during egg incubation

Colony (code)	Mean proportion (%) of time allocated to sleep behavior in 30 s recording				
	DI. diurnal (<i>n</i>)	NO. nocturnal (<i>n</i>)	DI. vs NO. comparison ^h <i>p</i> value	DINO—DI. and NO. combined (<i>N</i>)	DINO Significant contrasts ⁱ
Bydgoszcz–Konna (BYD-LP)	23.2 (1058)	49.9 (701)	<0.001	33.8 (1759)	a**, b**
Bydgoszcz–Stary Port (BYD-SP)	12.4 (443)	55.5 (570)	<0.001	36.6 (1013)	c**
Bydgoszcz–Przemysłowa (BYD-PR)	15.2 (430)	45.4 (715)	<0.001	34.0 (1145)	d***, e*
Koronowo (KOR)	24.2 (1499)	59.1 (1281)	<0.001	40.3 (2780)	a**, c**, d***, f***
Kusowo (KUS)	24.9 (180)	52.5 (79)	0.001	33.3 (259)	e*, g**
Skoki Duże (SKO)	28.7 (1469)	33.8 (1272)	1.0	31.1 (2741)	b**, f***, g**

N-sample size, i.e. number of 30 s recordings. Significance levels: **p*<0.05, ***p*<0.01, ****p*<0.001. Values: *a* 0.006, *b* 0.008, *c* 0.004, *d*<0.001, *e* 0.016, *f*<0.001, *g* 0.003

^hBeta regression, post-hoc estimated marginal means test

ⁱSignificant inter-colony contrasts, beta regression, post-hoc estimated marginal means test

colonies and the data recorded by GPS-tracked individuals from one colony (Fig. SM2, Supplementary Materials).

Factors affecting relative duration of sleep behaviour

We found that BHG partners that remained in nests during incubation of eggs spent on sleep $48.1 \pm 43.3\%$ (mean $\pm$ SD) of 30 s nocturnal recordings, and $23.5 \pm 35.3\%$ of 30 s diurnal recordings in each colony. This means that extrapolated time of sleep at night in these birds oscillated on average between 2.87 and 5.02 h (172–301 min). BHGs sleep over 31.1–40.3% of 30 s recordings depending on a colony. Beta regression model revealed that the relative duration of sleep during the incubation period was affected significantly by all studied predictors, i.e. colony (1–6), the part of 24 h (day/night), location of a nest in the colony (centre/peripheries) and interactions between these factors (Table 1). The noted inter-colony differences were significant (Table 1) with the highest value at Koronowo and the lowest one at Skoki Duże (Table 2). Regarding day/night differences (Table 1) BHG slept longer at night (mean $\pm$ SD: $48.0 \pm 43.3\%$ of 30 s recording) than during the day ($23.5 \pm 35.3\%$).

Location of nests within a colony had a significant effect on the relative length of birds' sleep (Table 1) with birds nesting in the centre sleeping longer (mean $\pm$ SD: $37.2 \pm 41.9\%$ of 30 s recording) than in the edge ($32.7 \pm 40.1\%$).

We found a significant interaction colony $\times$ day/night (Table 1). Post hoc tests revealed that in all colonies, except of Skoki Duże, duration of sleep did not differ between night and day (Table 2).

We found a significant interaction colony sector $\times$ day/night (Table 1). At night, BHGs that located their nests in the core centre of the island slept significantly longer

(mean $\pm$ SD $51.3 \pm 43.3\%$) than those that had nests at the edge of a colony ($43.8 \pm 42.8\%$; post hoc test, *p*=0.001). During the day birds nesting at the edge only tended to spend a higher proportion of time to sleep ($23.9 \pm 35.7\%$) compared to individuals from the edge ($23.1 \pm 34.8\%$; post hoc test, *p*=0.069).

We also found a significant interaction colony sector $\times$ day/night $\times$ colony (Table 1). Post-hoc tests revealed that generally the length of BHGs sleep during the day did not depend on nest location within the colony (post-hoc test, *p*=1.0) except for the colony at Kusowo, where birds slept longer at the peripheries, contrary to our expectations (Fig. 1). At night, only in two colonies, Bydgoszcz-Przemysłowa and Skoki Duże, birds at peripheries slept significantly shorter than these in the centre of the colony (Fig. 1). In other colonies, relative duration of sleep behaviour was similar at the edge and in the centre if the colony (post hoc test, *p*=1.0).

Analysis of daily distribution of sleeping behaviour of incubating individuals revealed that the proportion of time allocated to this behaviour was highest in the evening, moderate in early afternoon and lowest in the morning (Fig. 2). Moreover, we found that the distribution of sleep periods in subsequent time intervals during 24 h did not differ between the colonies (Anderson–Darling test *AD*=4.092, *p*=0.694). The location of a BHG nest in the centre or at the periphery of the colony also had no effect on 24 h distribution of sleep (Anderson–Darling test, *AD*=0.549; *p*=0.769).

Other activities of incubating individuals

Sleeping by BHGs on average over 48.4% of night means that they were active throughout the remaining part of a night. They spent most of this active time on passive and

Fig. 1 Proportion of time allocated to sleep in day and at night by black-headed gulls in relation to their nest location within a colony (centre vs edge). Red rectangles indicate significant differences

between colony sectors (beta regression, post hoc test, $p < 0.007$). Colony codes see Table 2 and Table SM1 in Supplementary Materials

active nest defence (mean = 73.2% and 7.3% of night time excluding sleep, respectively), and on maintaining the nest and arranging nest material (mean 10.6% of the night time excluding sleep) (Fig. 3). Proportions of time spent by birds on nest defence (passive and active combined) at night differed significantly between colonies (G test, $G = 22.263$, $df = 5$, $p = 0.0005$). During the day, gulls apart from sleeping spent most of this active time on passive or active nest defence (mean = 70.7% and 9.0% of the day excluding sleep, respectively) and on nest maintenance (mean = 15.1% of the day). The proportion of time allocated to nest defence (passive and active combined) during the day did not differ statistically between the colonies (G test, $G = 4.393$, $df = 5$, $p = 0.494$) (Fig. 3). BHG passively and actively defended and maintained nests in similar proportions of time at night and at the day ($G = 6.053$, $df = 5$, $p = 0.301$; $G = 3.342$, $df = 5$, $p = 0.647$; $G = 7.269$, $df = 5$, $p = 0.201$, respectively) (Fig. 3).

Differences between nocturnal and diurnal flights of GPS-tracked individuals

Analyses of GPS-tracking data revealed that after leaving the colony at night BHG crossed much shorter distance (total distance of flight) than at the day (linear mixed model, estimate = -0.731 , $df = 30.295$, $t = -2.310$, $p = 0.030$; Fig. 4a). We also found that the maximal range of nocturnal flights of BHGs were considerably shorter than daily flights (gamma regression, estimate = -0.892 , $df = 32$, $t = -3.629$, $p = 0.0003$; Fig. 4b), and that BHGs remained outside the breeding colony much longer at night than during the day (linear mixed model: estimate = 0.826 , $df = 34$, $t = 5.450$, $p < 0.001$; Fig. 4c).

Relationship between nocturnal and diurnal sleeping and various factors

We found that the duration of BHG's sleep during the day was significantly related to the density of nests in the colony (Pearson correlation, $r = -0.958$, $t = -6.726$, $df = 4$, $p = 0.002$; Fig. SM3, Supplementary Materials). In colonies

Fig. 2 Mean contribution of the sleeping behaviour of black-headed gulls per recording in particular time intervals over 24 h in each colony during egg incubation. Colony codes see Table SM1 in Sup-

plementary Materials. Time intervals: 5:30–7:00 (T1), 12:00–13:30 (T2), 18:30–20:00 (T3), 21:30–23:00 (T4), 00:00–1:30 (T5) and 3:00–4:30 (T6)

where the density of nests was the smallest birds slept over proportionally larger part of the day compared to birds breeding in the highest densities. However, we found no effect of nest densities on the length of BHGs sleep at night ($r=0.170$, $t=0.345$, $df=4$, $p=0.747$).

Moreover, we found that the amount of time allocated by BHGs to sleep during the day was significantly related to light pollution intensity around the colony after dusk (Pearson correlation, $r=-0.929$, $t=-5.031$, $df=4$, $p=0.007$; Fig. SM4, Supplementary Materials). In colonies where the light pollution intensity was the smallest birds slept over proportionally larger part of the day compared to birds breeding in the highest densities. However, we found no effect of light pollution intensity on the length sleep at night ($r=0.037$, $t=0.074$, $df=4$, $p=0.945$). We also found that the density

of nests in the colony was positively correlated with light pollution intensity around the colony after dusk (Pearson correlation, $r=0.925$, $t=4.874$, $df=4$, $p=0.008$).

Discussion

BHG is commonly considered a species of exclusively diurnal activity (Chandler 1983; Wikelski et al. 2006; Evans et al. 2018), but literature provides a few mentions their incidental nocturnal activity (Coward 1916; Beer 1962; Kruuk 1964; Hailman 1966). Our studies showed that at least during incubation of eggs, BHGs are active not only during the day, but are also regularly active after dusk, i.e. in late evening and night hours. This result is intriguing given the

Fig. 3 Relative duration of diurnal and nocturnal activities (other than sleeping) of black-headed gulls during egg incubation. Behaviour codes: *PDE* passive defence, *PRE* preening, *ADE* active defence,

OTA other activities, *NEM* nest maintenance, *SLE* sleep, *COA* common activities of a pair. Colony codes see Table 2 and Table SM1 in Supplementary Materials

fact that concentration of melatonin during 24 h in BHGs is relatively low compared to other gull species; it may enable BHGs to fall asleep easily at any time of day or night (and possibly guarantees their efficient restoration), and allowing to be ready for defend the nest with eggs or chicks during 24 h (Meyer and Millam 1991; John et al. 1993; Jessop et al. 2002; Wikelski et al. 2006).

Moreover, we found that the distribution of sleep periods and activity of BHGs in distinguished time periods (T1–T6) was similar in studied colonies, but their total sleep time at night differed between the colonies. These differences may be explained by various ecological and social conditions in colonies, naturally influencing birds' behaviour (e.g.

predation pressure, nest density, vegetation height and type and visibility of the surrounding area, time budget).

One of the studied factors, which might determine the length of sleep in BHG, was nest location. BHGs breeding in the centre of a colony slept longer at night than those that had nests at the edge of the island, as we expected. Birds at the peripheries of a colony were probably exposed to higher stress caused by potential danger from predators, and thus increased frequency or duration of vigilance periods, at the cost of rest and possibly restoration. This scenario seems the more probable as earlier studies showed that many bird species sleep less or shallower under predator danger (Lendrem 1983, 1984; Gauthier-Clerc et al. 1998, 2000, 2002; Dominguez 2003; Lima 2005; Diehl et al. 2020). Moreover,

Fig. 4 Characteristics of nocturnal and diurnal flights of GPS-tracked black-headed gulls breeding in the colony at Bydgoszcz (BYD-PR) during incubation period: **A** maximum range of flights (km), **B** total distance covered (km), **C** total trip duration (min). Boxplots show the

median (band inside the box), the first (25%) and third (75%) quartile (box), the lowest and the highest values within 1.5 interquartile range (whiskers) and outliers (dots)

the core of the colony usually offers the birds better protection against predators than peripheries. Colony centres are more difficult to access for predators, and higher density of breeding pairs in the centre enables more efficient detection of and deterring predators than at its edge (Davis and McCaffrey 1986; Becker 1995; Yorio and Quintana 1997; Velando and Freire 2001; Beauchamp 2009, 2012; Minias 2014). Because BHGs from the peripheries slept shorter at night, we expected they would compensate the night sleep deficit during the day and regenerate in this way. We thought this would be possible because during the day vigilance of each individual in a colony can be partly replaced with group vigilance, according to the rule “the neighbour sleeps, so do I” (Beauchamp 2009, 2011; Beauchamp et al. 2012; Evans et al. 2018), and such mechanism might promote more frequent and longer naps. However, contrary to our expectations, birds from colony’s edge did not compensate for their deficit of night sleep during the day. It is surprising, because long sleep deprivation leads to negative physiological consequences (Huber et al. 2004; Rattenborg et al. 2004; Snyder et al. 2013). Thus, it might be expected that BHGs that nest at the colony’s edge, despite shorter sleep at night, sleep sufficiently long or deep at the day. Perhaps only at the next life-stage, when energy expenses of adults are much larger than during incubation (they have to satisfy their own and chicks’

energy demands), the accumulated deficit of nocturnal sleep in individuals from colony’s edge might be compensated with longer diurnal sleep.

Probably, BHGs have a specific adaptation that enables them to shorten sleep at night without any loss of organisms’ functions during the day, analogously as in male pectoral sandpipers *Calidris melanotos*, which shorten sleep during competitive displays to increase breeding success and compensate for it with better quality sleep (Lesku et al. 2012). Another explanation for a lack of compensation for nocturnal sleep deficit might be unihemispheric sleep, detected in some avian species (Rattenborg 2006; Rattenborg et al. 2019). Possibly, BHGs also perform such sleep mode. However, neither the literature nor recordings from our camera traps provided any convincing evidence of unihemispheric sleep in BHGs. Our camera trap (set almost opposite to a sleeping bird or behind it) movies ($N=19$ recordings) have shown that only in 32% cases the bird certainly had one eye open and the other one shut, and in about 42% cases the bird had both eyes shut. Thus, we cannot state definitively that BHGs exhibited unihemispheric sleep in the colonies we studied. However, using such sleep by BHGs would likely enable full restoration of their organisms, as in e.g. great frigatebirds *Fregata minor* (Rattenborg et al. 2019); but see Rattenborg (2017) speculating that avian species may not

require restoration after sleep deprivation at the expected extent and compared to mammals.

Our studies also revealed an interesting relationship between the intensity of light after dark around the colony and BHGs' sleep during the day. Individuals breeding in colonies that were more illuminated at night (which were also characterized by a higher nest density) slept significantly shorter during the day than in darker colonies. Given the fact that light intensity at night had no effect on their sleep length at night, and that the nest density in the colony was positively correlated with light pollution intensity around the colony after dusk, it seems that effect of nest density was more important driver of diurnal sleep duration compared to night light pollution. Dense colonies may attract predators increasing birds' vigilance in fear of predator's attack, at the cost of duration and quality of birds' total sleep [including deep sleep (back sleep) and rest sleep (front sleep)]. Likely, birds in dense colonies more often interrupted sleep to observe neighbourhood, which may impede efficient restoration of their organisms (Raap et al. 2017). More studies are needed to fully comprehend link between light intensity, nest density and sleep duration. Those studies should include direct measurement of light level (it can be masked by high cloudiness, lush vegetation) and some important covariates as noise level, human disturbance level, predatory pressure.

We found that some GPS-tracked individuals left the breeding colony for the whole or a part of the nights. It confirms the previous observations in gulls; their staying outside the colony at night, especially at the first phase of settling on an island (Hébert and McNeil 1999), has been interpreted as anti-predator behaviour (Kruuk 1964; Mougeot and Bretagnolle 2000; Nisbet 1999; Diehl et al. 2020). Apart from this, some seabirds, as black-vented shearwaters or ring-billed gulls, during bright moonlight nights reduce their activity in a colony and even leave it to avoid a predator's attack, as compared to dark nights (Hébert and McNeil 1999; Keitt et al. 2004). Thus, spending the night during egg incubation on water and roofs of building by some studied BGHs individuals may be interpreted in context of seeking resting place safer from predators compared to the colony.

We are aware of some limitations of our study. We based our study on video recorded material with restricted camera view, thus we cannot say if the partner of the filmed individual is not sleeping just outside the camera frame. We did not marked individually birds so we are not sure which individuals from the pair was present in the frame. However, considering an equal contribution of both partners in incubation duties (Ytreberg 1956; Beer 1961), we assumed that there was no female or male bias in the analysed material. Given the lateral position of the eyes on the head, it is rarely possible to see both eyes of a bird with a single camera frame. Thus, we cannot excluded that we might not see some episodes of the unihemispheric sleep, especially

when only one side of bird was visible in the frame. We are aware that behaviour of the GPS-logger equipped individuals may be directly affected via expending extra energy counteracting both the additional mass and the increased drag, and decreasing some aspects of their performance, such as speed (Elliott et al. 2007; Vandenabeele et al. 2012). This bias might have affected the behaviour of the studied birds. We cannot exclude that birds in the first day after GPS-logger deployment behaved a little bit different than in the next day. Given small sample size we analysed data from all recorded days combined. We believe that the small size of the logger used (0.69% body mass of the captured individuals) should not affect birds' behaviour considerably. Moreover, we found that the hatching success in nests in GPS-logger equipped individuals was similar to the control group (see [Materials and methods](#)).

Nevertheless, our results represent the first systematic study on sleep in black-headed gulls and filled evident gap in knowledge about nocturnal behaviour of the studied species. More studies including hemispheric sleep is needed to fully comprehend sleeping behaviour of gulls.

In conclusion, we found that during the incubation period, BHGs were active at night (contrary to standard belief) and their activity can vary with colony density, location of nest site and lighting around the colony. Knowledge of the nocturnal behaviour of an organism is crucial to fully comprehend its 24 h activity patterns, especially to understand daily flexibility of behaviour types crucial for restoration, like sleep.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-021-01896-8>.

Acknowledgements We are thankful to colleagues from the Student's Zoological Science Club at the University of Science and Technology in Bydgoszcz who helped in the field work, especially to Aleksandra Kowalczyk and Malwina Pater. We are grateful to the Director of the Wdecki Landscape Park for a non-commercial lending of camera traps. We thank anonymous reviewers for constructive comments on the earlier draft of the manuscript.

Author contributions PI developed the concept of the study, collected data in the field, and drafted the manuscript, DJ performed statistical analyses, analysed GPS data and drafted the manuscript, JG analysed movies recorded by camera traps and collected data in the field. All authors read and approved the final manuscript.

Funding GPS-tracking was supported by the grant from National Science Centre (NCN), Poland, No. 2015/19/B/NZ8/01981.

Availability of data and material The datasets generated during and analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflicts of interests.

Ethics approval GPS-tracking of birds was conducted with the permission of Local Bioethical Commission for Animal Welfare in Łódź and Regional Environmental Protection Directorates in Bydgoszcz (Poland).

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