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Nocturnal Sleep Behavior and Vigilance of Incubating Common Terns (*Sterna hirundo*) at Two Inland Breeding Colonies

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Abstract.—Although sleep is necessary for maintaining physiological and cognitive function in birds, nocturnal sleep behavior has yet to be documented for terns. Nocturnal sleep behavior and vigilance of incubating Common Terns (*Sterna hirundo*) were explored at two colonies, Gull Island (Ontario, Canada) for six years, and Little Island (New York, USA) throughout one breeding season, using ~1-min interval, time-lapse images from infrared trail cameras. Behavioral posture and vigilance (eye[s] open) of visible study birds were recorded from the images to determine if these differed between the two colonies. Terns utilized two sleeping postures, Back Sleep and Front Sleep, nearly identical to those used by gulls. Differences in the proportion of time spent sleeping between the two colonies were surprisingly large. Terns at Gull Island spent 75% less time in Back Sleep (deep-sleep posture, 7% of the night) than those at Little Island, and 64% of night with their eyes open (vs. <20% at Little Island). Differences between the study sites that may have caused this disparity include predation risk, colony size, vegetation cover and the presence of other nesting waterbirds. Apparent, long-term sleep deprivation at Gull Island may have physiological impacts. Further research is needed to establish causes and effects of differences in nocturnal sleep behavior in Common Terns. *Received 16 July 2019, accepted 7 November 2019.*

Key words.—Black-crowned Night-Heron, Great Horned Owl, Intraspecific Sleep Variation, Nocturnal Behavior, Nocturnal Predation, Sleep Deprivation, Sleep Posture, Sternidae, Vigilance

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Sleep is a vital component of self-maintenance and plays an important role in energy conservation, cellular repair, and learning (Siegel 2005; Stuber *et al.* 2015). Severe sleep deprivation can reduce cognitive and physical performance (Huber *et al.* 2004), or may require compensatory adjustments at the expense of other activities (Fuchs *et al.* 2006). Sleep behavior varies considerably among bird species (Amlaner and Ball 1983; Campbell and Tobler 1984; Lesku *et al.* 2006). Amlaner and Ball (1983) describe sleep and rest postures for a range of species, including many waterbirds (predominantly gulls and ducks), finding similarities among closely-related species. In addition to evolutionary history, environmental factors such as light levels (Amlaner and Ball 1983), tidal state (Galusha and Amlaner 1978), predation risk (Lima *et al.* 2005), and social factors (e.g. Beauchamp 2011) can also strongly influence sleep.

Although sleep, rest and vigilance have been studied for several waterbird orders (Dewasmes and Telliez 2000; Gauthier-Clerc and Tamisier 2012; Handel and Gill 2012; Hayward *et al.* 2014), we are aware of only a single published study involving diurnal sleep in terns (Skipnes 1983) and none for nocturnal sleep (although see Weseloh & Shutt [2008] for roosting behavior prior to sleep). Across the day, Skipnes (1983) recorded an average of 13.9-35.6% of birds in a sleeping posture equivalent to Back Sleep as reported in other species (Amlaner and Ball 1983), with fewer birds sleeping late in the day. Contrastingly, large gulls (genus *Larus*) have been the focus of many studies (Galusha and Amlaner 1978; Bartholomew and Dawson 1979; Amlaner and McFarland 1981; Amlaner and Ball 1983), but these species may differ from terns in their sleep behavior because of disparities in exposure to interspecific predators at breeding colonies (Beauchamp 2011), preferences for nesting vegetation (Fasola and Canova 2006), or diet and daily activity cycles (Pearson 1968; Fasola and Bogliani 1990). The absence of information on nocturnal sleep represents an important knowledge gap, particularly for Common Terns (*Sterna hirundo*), because nocturnal predation is a major cause of breeding failure (Cuthbert *et al.* 2003; Nisbet *et al.* 2017). Thus, understanding sleep behavior and vigilance may have significant conservation value.

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Many studies have reported effects of predators on sleep behavior. Under immediate (or perceived) predation threat, birds alter sleeping postures, becoming more vigilant (changing from deep-sleep to rest-sleep postures, opening eyes) and reducing rates of eyelid closure (Amlaner and McFarland 1981; Lendrem 1983, 1984). Other factors that may affect sleep include nesting habitat, colony or group size, and the presence of other nesting waterbirds. Vegetation cover at nest sites has been found to interact with predation risk, increasing vigilance of incubating Mallards (*Anas platyrhynchos*) when line-of-sight is blocked (Javůrková *et al.* 2011). Increased group size also affects vigilance as lower levels are required of an individual, per capita predation threat may be reduced ("dilution effect"), and many potential prey may create confusion for hunting predators (Foster and Treherne 1981; Beauchamp and Ruxton 2008, 2012). Reduced necessity for watchfulness may lead to increased sleep or different sleep behaviors (Gauthier-Clerc *et al.* 1998, 2002; Dominguez and Dominguez 2003; Lima *et al.* 2005). Advantages of group size might also be derived from nesting in mixed-species colonies, assuming that information about predation risk can be interpreted from other species (Beauchamp 2011).

We studied nocturnal sleeping postures of incubating Common Terns and explored variation in sleep and vigilance for six breeding seasons at Gull Island, Ontario, a small mixed-species colony in Lake Ontario. To examine whether sleep behaviors and vigilance varied between colonies, in 2018, we also collected the same data at a larger, single-species breeding colony at Oneida Lake, New York State, USA. At both colony sites, we used data concerning eye closure and posture to provide a first description of nocturnal sleep behavior of incubating Common Terns and its variability.

METHODS

Study Area

We studied incubating Common Terns at Gull Island, Presqu'ile Provincial Park, Ontario, Canada (43° 59′ 6.0″ N, 77° 44′ 12.0″ W) for 6 years (2013-2018 inclusive) and at Little Island, Oneida Lake, New York, USA (43° 14′ 12.0″ N, 76° 0′ 0.0″ W) in one year (2018). Both sites have supported an active tern colony almost annually since the 1950s (Courtney and Blokpoel 1983). During the study, 57-88 pairs of Common Terns nested at Gull Island (June peak counts) in an area of ~200 m^2. On the 0.1-hectare Little Island, 369 tern nests were counted on 3 July (peak summer count) in 2018, which is close to the long-term average. Gull Island also supported approximately 20,000-30,000 pairs of breeding Ring-billed Gulls (*Larus delawarensis*), 100 pairs of Herring Gulls (*L. argentatus*), 600-700 pairs of Caspian Terns (*Hydroprogne caspia*), and up to 6,000 pairs of Double-crested Cormorants (*Phalacrocorax auritus*), whereas Little Island was a single-species colony. Common Terns on Gull Island suffered from a high level of nest predation, both during the study and historically (Morris *et al.* 1980), mainly from Black-crowned Night-Herons (*Nycticorax nycticorax*) (all study years) and Great Horned Owls (*Bubo virginianus*) (2016 and 2017 only). Terns on Little Island have historically experienced only occasional predation, last documented in 2015 when a Great Blue Heron (*Ardea herodias*) visited the colony at night.

Management for Common Terns at both sites incorporates use of a grid of parallel overhead polywires, but with different designs for different purposes. At Gull Island, annually since 2014, parallel wires ~0.3 m apart are strung over a nesting area fenced with shade cloth or plywood-and-hardware-cloth after the terns are established to prevent entry by Black-crowned Night-Herons in June and July (gridded nests not in study, see below). At Little Island, parallel wires ~1 m apart are erected in April with no perimeter fence, to prevent nesting by Ring-billed Gulls and allow terns to become established as nesters.

Field Methods

We used infrared trail cameras to monitor Common Tern nests during the breeding season (14 May-4 Aug). We used Bushnell Trophy Cam 119456C, Trophy Cam HD Max 119576C, Aggressor 119774C (Overland Park, Kansas, USA), Stealth Cam STC-DS4K (GSM Outdoors, Grand Prairie, Texas, USA), and Browning Recon Force BTC-2 (Morgan, Utah, USA) trail cameras equipped with automatic triggering of infrared flash based on external light intensity. We mounted cameras on steel rebar, fencing, or tree branches at elevations from > 0.5 m to < 2 m and within 1-5 m from nesting Common Terns, to provide a clear view of as many nests as possible. The number of cameras deployed simultaneously varied between one and six, but not all were used for observing nocturnal sleep (some cameras were deployed in a way that maximized detection of nest predators). We programmed cameras to take photos at 1-minute intervals throughout the night from 20:00 to 08:00 hr ("nocturnal images") and during the day in most years, which allowed us to detect when nests became permanently abandoned. At both sites, nests within

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the camera view were marked with individually numbered stakes behind the nest. Once eggs from nests within camera view started to hatch, leaving fewer incubating birds visible, we moved the camera to a new location overlooking later-incubating terns. We visited colonies and checked contents of study nests once every 1-5 d at Gull Island (but commonly at least every other day, weather depending) and every 3-4 d at Little Island. During each visit, we recorded whether each nest was still active and changed batteries and memory cards in trail cameras as needed.

Data Processing

Over 1.3 million images were captured, and all nocturnal images were visually checked for presence of nest predators, periods when active nests were unattended, adverse weather (rain and wind), and flooding from high water events. Prior to extraction of data on nocturnal posture and vigilance, we excluded any camera-nights without a complete sequence of nocturnal images: uninterrupted images at 1-min intervals throughout the nocturnal period. This period was defined as from 30 min after infra-red flash activation to 30 min prior to flash deactivation. We also excluded any camera-nights when no visible terns were actively nesting or visible terns were within management grids of the Gull Island colony, since grids on this island were designed to protect terns from predators and may potentially influence vigilance and sleep behavior.

Study nests were then determined prior to data extraction for each sequence of images taken within the same field of view, often over multiple nights. Two criteria determined study nests: birds at study nests were consistently visible (i.e., not obscured by vegetation or other birds) over a series of images taken throughout the sequence, and they were close enough for eye closure to be detectable on images (≤ 7 m from the camera). Any nests that became permanently abandoned before or during observation periods were excluded from the study. Nocturnal posture and vigilance (see Analyses) were recorded for birds incubating at study nests ("study birds") between the onset of darkness and dawn, defined as 30 min after infrared flash activation and 30 min prior to infrared flash deactivation. Number of study birds during each sequence ranged from 1-4 at Gull Island and 1-3 at Little Island over the nights that fulfilled all the above criteria (83 at Gull Island, 40 at Little Island).

In each image, the behavioral posture of each study bird was assigned to one of the categories described by Amlaner and Ball (1983) for sleep postures across the class Aves (illustrated in Fig. 1), and we also recorded whether at least one of each study bird's visible eyes was open or closed. If neither of the bird's eyes were visible temporarily, e.g., bird with back to camera, we excluded this record. Electroencephalographic measurements have shown that eye closure and sleep are closely related (Rattenborg *et*

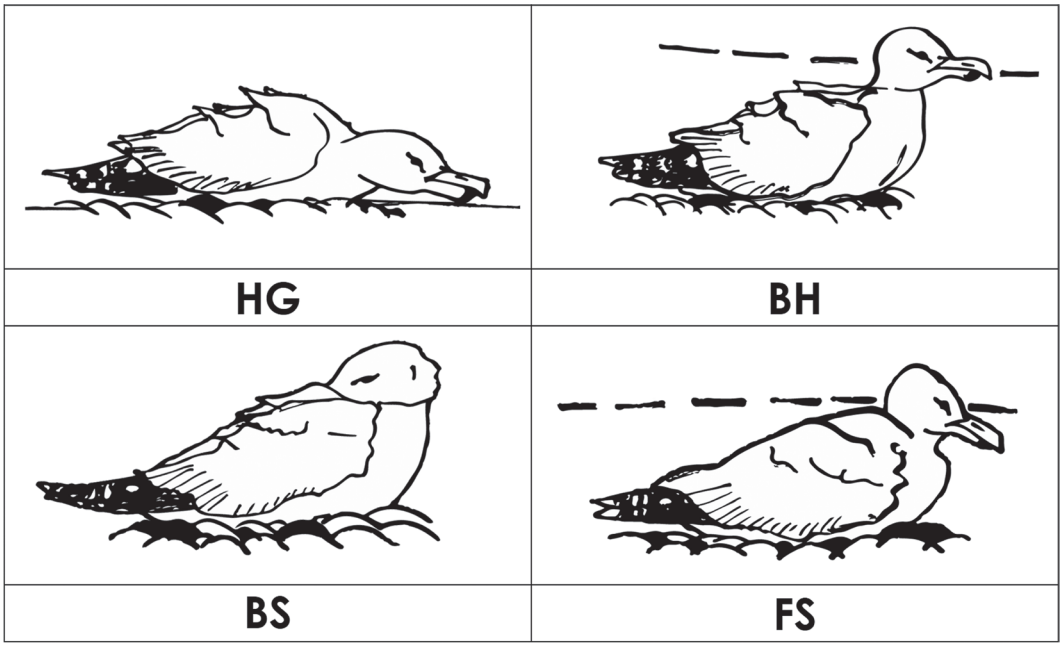


Figure 1. Possible sleep postures used by waterbirds, illustrated for gulls (in which all behaviors except HG have been recorded [Amlaner and McFarland 1981; Amlaner and Ball 1983; Henson *et al.* 2007]): HG = Head on Ground; BH = Bill Horizontal (bill in line with or above body axis); BS = Back Sleep (head turned back, bill on back and/or tucked under scapulars); and FS = Front Sleep (head drawn slightly in, bill below horizontal body axis). Illustration by Zoe Korpi.

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al. 1999), making eye closure a reliable indicator of sleep in birds (Amlaner and Ball 1983; Campbell and Tobler 1984; Wellmann and Downs 2009). Finally, we recorded the number of study birds that were visible but standing away from their nests ("off the nest") and images in which all study birds were absent (as a proxy for nocturnal desertion).

Data Analyses

We present sleep posture data for each colony as proportional use of all behavior posture categories: Back Sleep (BS), Front Sleep (FS), Head on Ground (HG), and Bill Horizontal (BH) (Fig. 1) across all study nights, further subdividing these according to whether birds' eyes were open (O) or closed (C). To be conservative, we combined BH behavior with other wakeful activities (e.g. preening, calling, etc…) as a single category, Non-sleep behavior (NS). Thus, each incubating bird was assigned to one of eight categories: BS-O, BS-C, FS-O, FS-C, HG-O, HG-C, NS-O and NS-C. We define sleep as: BS-C, FS-C, or HG-C; and vigilance as BS-O, FS-O, HG-O, or NS-O.

To examine the possible influence of predation risk between sites and within a site (Gull Island), we estimated daily levels of predation risk using historical records from each colony site, and direct and indirect evidence of predator activity. Historically, few incidences of nocturnal predation have been reported at Little Island; in 2018, no evidence of nocturnal predation was detected. Data from Little Island (n = 40 nights) were therefore categorized as "No Predation Risk". Gull Island has frequent nocturnal predation (Arnold *et al.* 2016), with regular losses from the Black-crowned Night-Herons (leading to complete colony failure in some years), and occasional visits from Great Horned Owls. However, the immediate presence of a predator is likely to have a very different impact on behavior than simply an earlier occurrence (Hunter and Morris 1976; Nisbet and Welton 1984; Arnold *et al.* 2006). Thus, we assigned data from Gull Island into two categories. "Immediate Predation Risk" included data from nights when a predator was visible in images from any cameras deployed in the colony, not just those analyzed for sleep behavior (see Field Methods), or from field signs such as predated or missing eggs or chicks detected during a nest check on the following day (n = 8 nights). "No Immediate Predation Risk" included data from all other nights in which no egg or chick loss was detected in a subsequent nest check (n = 13 nights) and excluded any nights on which this determination could not be clearly made. We then calculated nightly means of Proportional Vigilance (proportion of visible study birds that were vigilant in an image), testing for differences in this metric among these three predation risk groups in ANOVA with Tukey post-hoc tests. We chose to use eye opening rather than sleep posture for this analysis because vigilance is strongly, inversely correlated with sleep behavior (Amlaner and McFarland 1981; Lima *et al.* 2005), and lends itself better to simple analysis than multiple sleep/rest postures that may signify different, but variable, degrees of sleep (Amlaner and McFarland 1981). All statistical analyses were performed in R (R Core Team 2018).

RESULTS

Only two (Back Sleep, BS and Front Sleep, FS) of the four potential sleep postures (Fig. 1) were used for nocturnal sleep by incubating Common Terns in our study. There were large differences between our two study colonies in the proportion of time spent by Common Terns in different sleep behaviors (Fig. 2), with much less sleep at Gull Island (22% of noctur-

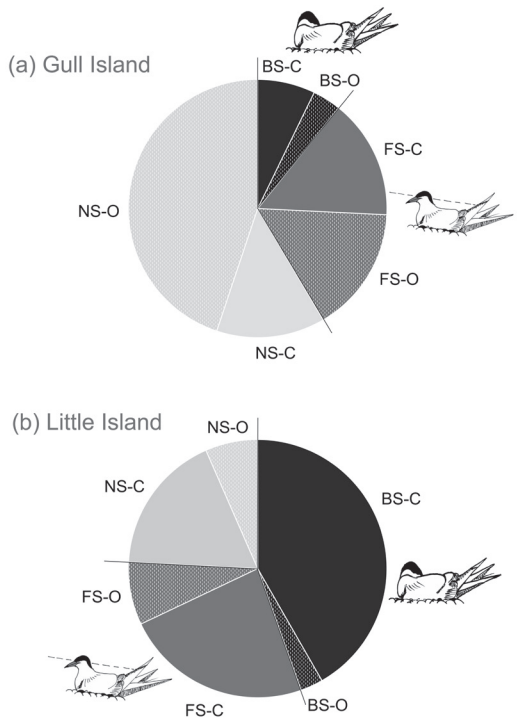


Figure 2. Relative proportions of time spent by incubating Common Terns in three categories of behavioral posture at (a) Gull Island and (b) Little Island during nocturnal hours. These categories are further subdivided according to whether at least one eye was open (-O, strippled fill) or not (-C, solid fill). Time spent off the nest is excluded from these graphs but accounted for <1%. NS represents non-sleep behaviors, predominantly BH with eyes open, but a small proportion of other behaviors, e.g. calling. HG postures were never observed. Illustration by Zoe Korpi.

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nal hours vs 65% at Little Island), of which only 7% were deep sleep (Fig. 2). Common Terns at Gull Island were far more vigilant than those at Little Island (64% vs. 17%) and spent less time with eyes closed in Back Sleep (the deepest sleep posture) (7% vs. 42%, Fig. 2). Proportion of time spent in Back Sleep was 75% lower at Gull Island than at Little Island. Terns at both colonies spent a similar proportion of time in Front Sleep, but at Gull Island they were twice as likely to have open eyes in this posture (Fig. 2). Overall, Common Terns incubating at Gull Island were vigilant for 63.7% of the night versus only 17.2% at Little Island (Fig. 2).

Nightly Proportional Vigilance varied between predation risk categories ($F_{2, 58}$ = 94.5, $P < 0.001$), although the only statistically significant differences were those between "No Predation Risk" (Little Island) and the other two categories (Gull Island). Much overlap existed in Proportional Vigilance between nights classified as "No Immediate Predation Risk" and "Immediate Predation Risk" (Fig. 3), both categories comprising data from Gull Island only. Periods of nocturnal desertion by birds at all visible study nests were highly variable across nights, and the mean proportion of a night deserted (mean ± SD) was 0.21 ± 0.18 for "No Predation Risk", 0.21 ± 0.28 for "No Immediate Predation Risk", and 0.32 ± 0.29 for "Immediate Predation Risk".

DISCUSSION

To date, no quantitative data have been published on nocturnal sleep posture in terns. Our results indicate that Common Terns utilize Back Sleep and Front Sleep, which are sleep/rest postures reported for many bird species (Amlaner and Ball 1983). In Back Sleep, Common Terns turned their head backwards and tucked their bill under their scapulars to differing degrees. In Front Sleep, the head was forward, but drawn in slightly, and the bill hung below the horizontal body axis. These two postures are nearly

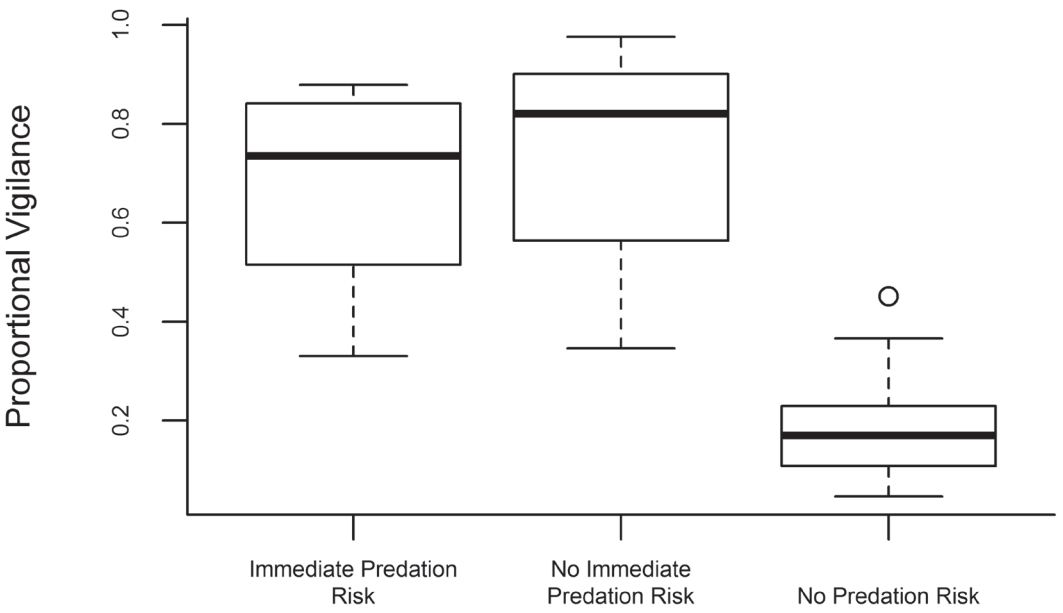


Figure 3. Boxplot of proportion of incubating Common Terns recorded with eye(s) open ("Proportional Vigilance") during nocturnal hours at Gull Island when a predator was likely present ("Immediate Predation Risk", *n* = 8 nights), at Gull Island when no predator was present ("No Immediate Predation Risk", *n* = 13 nights) and at Little Island when no predator was present ("No Predation Risk", *n* = 40 nights). Circles indicate outliers: 1.5 × interquartile range above the upper quartile.

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identical to those recorded for sleep/rest in closely-related species, such as gulls (Bartholomew and Dawson 1979; Amlaner and McFarland 1981; Amlaner and Ball 1983; Shaffery *et al.* 1985) and shorebirds (Dominguez and Dominguez 2003; Handel and Gill 2012). In Herring Gulls, for example, the deepest sleep posture is Back Sleep, where the bill is tucked under the scapulars, while Front Sleep, with the head drawn into the breast and head and bill slightly lowered, is a rest-sleep posture (Amlaner and Ball 1983, Amlaner and McFarland 1981). Slight variations of these two postures are also common among less closely-related waterbirds, such as ducks and penguins (Amlaner and Ball 1983; Stahel *et al.* 1984; Dewasmes and Telliez 2000), as well as distantly-related species, such as raptors and passerines (Amlaner and Ball 1983). Thus, these sleep postures are likely to be derived largely from shared evolutionary history and/or morphological constraints of body design.

Common Terns at Gull Island were far more vigilant than those at Little Island and spent less time with eyes closed in Back Sleep (the deepest sleep posture). These differences were surprisingly large, and because Common Terns at Gull Island slept barely one-third as much as terns at Little Island this could possibly lead to long-term physiological impacts (Huber *et al.* 2004) or necessitate compensatory mechanisms (e.g., increased diurnal sleep, Fuchs *et al.* 2006). Such differences between sites also indicate that in terns, as in other species (Rattenborg *et al.* 2017), prevailing environmental factors may play an important role in determining nocturnal sleep.

Because predation risk is one of the best studied and most commonly reported factors influencing sleep (Lima *et al.* 2005), we attempted to examine the effect of predation risk separate from the other factors that varied between our two colonies. However, because our two colonies differed in other factors that may have affected sleep behavior (colony size, vegetation, other nesting waterbirds), we could not fully dissociate the effects of predation from other site differences. By categorizing Gull Island observations as either "Immediate Predation Risk" or "No Immediate Predation Risk", we expected vigilance to decline following this order (as in other studies, Lima *et al.* 2005; Stuber *et al.* 2014) and be lowest at Little Island, where nocturnal predation was not recorded in the year of study ("No Predation Risk"). Even though vigilance was lower at Little Island, lack of a significant difference between "Immediate Predation Risk" and "No Immediate Predation Risk" categories (both from Gull Island, Fig. 3) does not strongly implicate predation as driving vigilance differences between our two sites. It is possible that this result may be confounded if nightly sleep is already constrained to its required minimum levels at Gull Island (preventing elevated response under immediate predation threat), or if terns respond to nocturnal predation up to a week after a predator's final visit (e.g., Hunter and Morris 1976; Nisbet and Welton 1984; Wendeln and Becker 1999; Arnold *et al.* 2006), thus obscuring vigilance differences on nights categorized as "No Immediate Predation Risk". Periods of nocturnal desertion showed a different trend, being only longer on nights of "Immediate Predation Risk" but were too variable to permit a statistical comparison of appropriate power.

Aside from predation risk, possible explanations for disparity in sleep between our two study colonies are differences in colony size (Beauchamp and Ruxton 2012), vegetation cover (Javůrková *et al.* 2011), and proximity to other species (Roberts 1996). Our data were insufficient to examine colony size effects distinct from predator effects, because nights with substantially different colony sizes were rare. Vegetation close to nests has been reported to increase vigilance behavior in nesting Mallards, whose nest predators primarily use olfactory cues (Javůrková *et al.* 2011). Night-herons and owls hunt by auditory or visual detection (Hunter and Morris 1976; Nisbet and Welton 1984) and terns, like gulls (Ball *et al.* 1984), probably also use auditory and visual cues to detect predators. Thus, although extensive and tall (>1 m) vegetation decreases the chance of being seen by a predator, it also requires that terns rely more on auditory predator detection, which may increase vigilance (Ball *et al.* 1984). In-

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creased vigilance at Gull Island supports this idea, but vegetation effects are largely confounded with predation risk because of the absence of predation at Little Island in our study. Alternatively, it is possible that the presence of 20,000-30,000 nesting Ring-billed Gulls at Gull Island may be responsible for increased vigilance. Ring-billed Gulls compete with Common Terns for nest sites (Cuthbert *et al.* 2003; Morris *et al.* 2010), can eat tern eggs (Nisbet *et al.* 2017), and also provide constant noise (ranging from 77.4 - 102.5 dB, Blokpoel and Neuman 1997) that may hamper auditory surveillance against predators.

In addition to providing the first detailed description of nocturnal sleep behavior in terns, we found that the extent of nocturnal sleep achieved by incubating Common Terns varied greatly between colonies; it was notably very low at Gull Island (deepest sleep during <7% of nocturnal hours). Because sleep deprivation can lead to physical and cognitive impairment (Huber *et al.* 2004), and may require compensatory diurnal sleep that reduces provisioning rates and vigilance (Fuchs *et al.* 2006), our results call for a deeper exploration of these potential consequences as well as the possible factors influencing sleep in terns.

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