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Nocturnal Behavior of Wintering Common Cranes (*Grus grus*) Under Varying Environmental Conditions

 Flavio Monti¹  | Marco Ciolfi¹  | Giuseppe Anselmi² | Niccolò Fattorini³  | Francesco Ferretti^{3,4} 

¹Research Institute on Terrestrial Ecosystems (IRET), National Research Council (CNR), Porano (TR), Italy | ²Maremma Regional Park Agency, Alberese (GR), Italy | ³Department of Life Sciences, University of Siena, Siena, Italy | ⁴NBFC, National Biodiversity Future Center, Palermo, Italy

Correspondence: Flavio Monti (flavio.monti@cnr.it)

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ABSTRACT

Nocturnal conditions impose strong constraints on diurnal species, requiring behavioral adjustments to balance predation risk and social interactions. We investigated how environmental factors shape nocturnal behavior in wintering Common cranes [*Grus grus* (Linnaeus, 1758)] in central Italy during the 2022–2023 season, using an integrated approach combining camera trapping and acoustic monitoring. We quantified activity, vigilance, display, and vocal behavior in relation to night phase, moon illumination, cloud cover, and seasonal progression. Cranes exhibited high nocturnal activity overall ($89.4\% \pm 2.1\%$ of individuals per night), with $44.8\% \pm 3.9\%$ showing vigilance. Activity peaked toward morning but decreased significantly with increasing moon illumination, and this effect was partially buffered by cloud cover. Vigilance followed a similar pattern, declining under bright conditions and increasing during darker periods, consistent with antipredatory responses. In contrast, display behavior was positively associated with moon illumination and increased over winter, indicating that cranes exploit illuminated conditions for visually mediated social signaling, possibly in preparation for migration. Vocal activity showed the opposite trend, being higher in darker conditions, indicating its role in maintaining social contact when visual communication is limited. Overall, Common cranes exhibit pronounced nocturnal behavioral flexibility, modulating different behavioral components in response to environmental cues. These findings show how external *stimuli* can act as selective forces shaping nocturnal strategies in diurnal species.

1 | Introduction

For diurnal species, nighttime constitutes a critical ecological boundary. Their sensory systems, circadian rhythms, and behaviors are optimized for daylight, making darkness a period of heightened vulnerability (Beauchamp and McNeil 2003; Tillman 2009; Yorzinski and Platt 2012). Reduced light conditions impair visibility, which decreases the ability to detect landscape cues essential for spatial orientation and efficient foraging (Bayne and Brigham 1995; Camacho et al. 2026) as well as increases predation risk (Monterroso et al. 2013) and the likelihood of incurring unexpected hazards (e.g., vehicle collisions; Cerri et al. 2023). Loss of visual contact with conspecifics further

threatens gregarious species (Perret et al. 2015). Diurnal species are typically expected to sleep and consolidate their resting activity at night (Aulsebrook et al. 2021). Although resting is essential, it also increases vulnerability to predation (Lima 2009). The presence of nocturnal predators, combined with a reduced visual ability, compels wild prey to employ compensatory antipredator strategies, which can constrain the timing and organization of other fitness-related behaviors, including foraging and resting itself (Beauchamp 2015). In dynamic environments, diurnal species must continually balance trade-offs between behaviors (Dunbar et al. 2009). This balance between rest and antipredatory behavior is a fundamental ecological challenge and a key axis of behavioral adaptation (Lima 2009; Aulsebrook

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et al. 2021). Night is hence not merely the absence of light but a selective pressure shaping behavior, survival, and life-history traits (Beauchamp 2007; Penteriani and Delgado 2017).

To cope with nighttime risks, diurnal animals have evolved a wide range of anti-predatory strategies (Fichtel 2007; Yorzinski and Platt 2012), aimed at optimizing the trade-off between rest and alertness. Prey species may select for refuges or shelters, such as caves, tree cavities, vegetation cover, or water bodies (Manser and Bell 2004; Tsurim et al. 2010), as well as for “temporal refugia.” For example, mammals often shift from nocturnal to crepuscular or diurnal activity to avoid nocturnal predators (Monterroso et al. 2013; Lazzeri et al. 2024). Conversely, some species may increase nocturnality in response to diurnal human disturbance/predators (Gaynor et al. 2018). In the absence of predators, antipredator behavior generally becomes more relaxed (Bannister et al. 2018). Some species rely on specialized communication to warn conspecifics and maintain social contact in low-light conditions (Fichtel and Kappeler 2002; Sierro et al. 2024). Vigilance is another major antipredator behavior, which can also facilitate social communication, intraspecific interactions, and resource acquisition (Beauchamp 2009). While vigilance provides survival benefits, it incurs energetic costs, as time and attention allocated to scanning are subtracted from other activities. These trade-offs can affect individual survival and population dynamics, with cascading conservation implications (Watson et al. 2007; Beauchamp 2010). Variation in vigilance occurs among sexes (Powolny et al. 2014), age classes (Boukhriss et al. 2007), or both within and among individuals (Beauchamp 2010), particularly in social species where group dynamics mediate collective antipredatory responses (Manser and Bell 2004; Boukhriss et al. 2007; Monti et al. 2024). Vigilance is further modulated by predation risk and disturbance (Diehl et al. 2020; Yorzinski and Platt 2012; Li et al. 2017), group size (Monti et al. 2024), habitat structure (Gou et al. 2022), and light conditions (Kramer and Birney 2001; Prugh and Golden 2014).

Among birds, this balance between resting and vigilance has been the subject of increasing ecological interest (Fernández-Juricic 2012). Avian species exhibit a variety of adaptive responses to nocturnal vulnerability, including changes in posture, flocking behavior, sentinel systems, communicative repertoires, and roost-site selection (Mougeot and Bretagnolle 2000a; Caro 2005; Budka and Kokociński 2021; Gong et al. 2024). Despite extensive research on diurnal vigilance (Li et al. 2015; Beauchamp 2015; Brereton and Rose 2019; Monti et al. 2024), studies addressing nocturnal antipredator behavior under field conditions are relatively scarce (Beauchamp 2007; Gong et al. 2024). Most existing studies rely on artificial or semi-natural settings (van Hasselt et al. 2020a, 2020b), allowing experimental control (Rose et al. 2018). However, a recent systematic review has shown that wild and zoo-housed animals may significantly differ in their time-activity budgets (Kelly et al. 2025). Understanding how diurnal species adjust their vigilance and resting patterns in response to nighttime risks is essential for elucidating the ecological and evolutionary bases of anti-predatory strategies in natural environments. This knowledge gap underscores the need for field-based investigations integrating behavioral observations with environmental variables to assess nocturnal antipredatory behaviors under realistic ecological contexts.

Environmental factors are particularly relevant in this context, operating across multiple spatial and temporal scales. Nighttime visibility is influenced by light conditions and can modulate animal behavior, including antipredator tactics (Mougeot and Bretagnolle 2000b; van Hasselt et al. 2021). Light conditions, including photoperiod and lunar phase, regulate circadian rhythms and influence the duration, timing, and intensity of both activity and rest (Aulsebrook et al. 2020a, 2020b; van Hasselt et al. 2020a). As the primary source of natural illumination, moonlight plays a key role in determining nighttime brightness and visibility (Penteriani and Delgado 2017; van Hasselt et al. 2021), while its predictable cycle may provide a reliable environmental cue for behavioral synchronization. Bird sleep is strongly affected by environmental conditions such as nighttime light levels (Aulsebrook et al. 2020a, 2020b), including effects of artificial lights at night (Aulsebrook et al. 2021). Evidence from semi-natural conditions suggests that increased moon illumination can reduce sleep duration (e.g., Barnacle geese, *Branta bernicla*, and European starlings, *Sturnus vulgaris*; van Hasselt et al. 2020a, 2020b).

Seasonal and temporal variables, such as variation in day length and migratory phase, may interact to shape activity and resting patterns over both short- and medium-to-long-term scales (e.g., Newton 2010; van Hasselt et al. 2020b). Migratory species adjust their resting patterns to meet increased energetic demands (Newton 2010). Such changes often include extended nocturnal activity (e.g., migratory restlessness; Berthold 2001). Thus, understanding how diurnal birds navigate the trade-off between activity and rest during the night likely depends on the complex interplay of ecological, physiological, and behavioral factors. Investigating nocturnal activity in diurnal species is essential for elucidating the adaptive significance of these behaviors.

In this study, we assessed how the phase of the night, moon illumination, and seasonal progression influence nocturnal activity, vigilance, and the occurrence of social behaviors (displays and vocalizations) in a diurnal bird species, the Common crane [*Grus grus* (Linnaeus, 1758)], at a coastal Ramsar site in central Italy. Based on previous findings of minimal daytime resting in the same population (Monti et al. 2024), we hypothesized that cranes would be largely inactive at night while retaining context-dependent antipredator behaviors such as vigilance and acoustic signaling. Given their gregarious nature, we also examined whether typically diurnal behaviors, including social interactions or displays, occur nocturnally (Ellis et al. 1998; Dinets 2013).

Based on these premises, we investigated whether nighttime (a) activity, (b) vigilance, (c) display behavior, and (d) vocal behavior were influenced by (x) the phase of the night, (y) the interaction between moon illumination and cloud cover, and (z) seasonal progression. We first hypothesized that (x) would influence (a), (b), (c), and (d), as diurnal species typically follow daily rhythms driven by light fluctuations. We predicted that: (P_i) the highest (a), (b), (c), and (d) levels occurred at dusk and dawn and would be lowest during the night, in accordance with the general assumption that diurnal species consolidate their resting activity at night (Aulsebrook et al. 2021). Then, we hypothesized that (y), a key determinant of visibility (Śmielak 2023), would modulate all behaviors. Specifically, we predicted that: (P_{ii}) higher

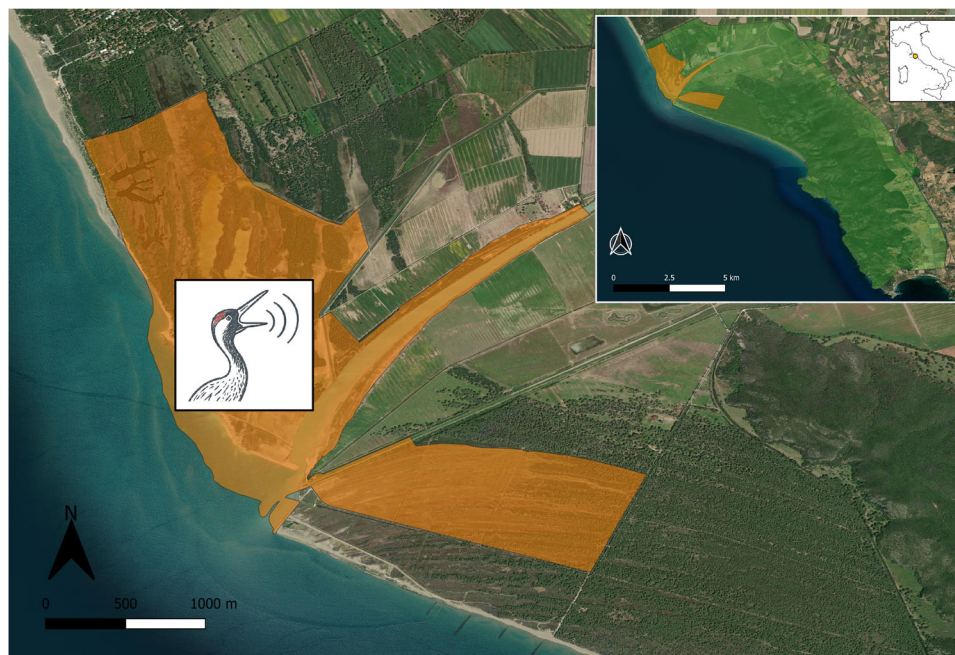


FIGURE 1 | Study area within the Ramsar site “Trappola Marshland—Ombro River Mouth” (light orange). The inset shows the location of the Ramsar site within the Maremma Regional Park (light green) and the location of the Park (orange dot) in central Italy.

moon illumination, because of higher visibility, would promote an increase of (a), (b), (c), and (d), enhancing social interactions in this gregarious species, while simultaneously reducing rest (van Hasselt et al. 2020a, 2020b). Conversely, cloud cover, which reduces sky brightness by blocking lunar and starlight (Jechow et al. 2019), was expected to counteract this process, by limiting all behaviors and promoting rest, although moon illumination may be a stronger driver of nocturnal activity than cloud cover (e.g., Lermineaux et al. 2025). Finally, given that the Common crane is a migratory species, we hypothesized that (z) would affect all behaviors, varying with time since arrival at the non-breeding grounds. Accordingly, we predicted that: (P_{iii}) all the activity indices increased as winter progressed, because of migratory restlessness, and peak before migration.

To fully comprehend these dynamics, we applied an integrative approach, linking behavioral, ecological, and environmental dimensions, with the aim to elucidate mechanisms and evolutionary drivers shaping nocturnal behavior in this diurnal species.

2 | Materials and Methods

2.1 | Study Area

Our study was conducted in a coastal wetland at the mouth of the Ombro River, in the northern sector of the Maremma Regional Park (42°39'N, 11°05'E) (Figure 1). The area is designated as a Wetland of International Importance (Ramsar site no. 2284—<https://rsis Ramsar.org/ris/2284>). The area has a typical Mediterranean climate, with mild winters (mean daily temperature in the period December 2022–March 2023: ~10.4°C and mean daily rainfall of ~2.24 mm for the same period; data from Alberese weather station [TOS11000103]: <https://sir.toscana.it>). Located within a

strictly protected zone within and far from urban centers, the site is free from light pollution, particularly in winter when coastal recreational activities are absent, thus representing a largely undisturbed natural setting. The wetland is an important regional wintering ground for cranes and Grey-lag geese [*Anser anser* (Linnaeus, 1758)], hosting up to 600 and 3300–3700 individuals, respectively (Giovacchini 2019; Monti et al. 2024). From central-northern Europe, cranes arrive in early November, although arrivals continue until early December, and remain until early March (Mingozzi et al. 2013; Giovacchini 2019). During the daytime, they leave the communal nocturnal roost to forage in nearby open fields (Monti et al. 2024). Potential predators occurring in the study area include wolves *Canis lupus* and red foxes *Vulpes vulpes*. Diet studies indicate limited predation on birds by wolves (~1% of scats in winter; $n = 189$; Ferretti et al. 2019) and a higher occurrence in fox diets (~13%; $n = 299$; Ferretti et al. 2021), although species-specific predation on cranes has not been quantified.

2.2 | Field Sampling Protocol

Data collection was conducted at the main nocturnal roost from December 15 2022 to March 15 2023. Sampling began in mid-December to ensure that migration had concluded, and only overwintering individuals were present. Up to five cameras (model: Conmitel Micro-Guard 2) were deployed simultaneously. Cameras were mounted on poles ~1 m above ground and spaced 160 ± 85.3 m (SD) apart, each oriented toward distinct, non-overlapping sections of the roost to maximize spatial coverage of the focal area. Water depth in the area varied with rainfall but did not exceed 1 m. Each camera was powered by an external 12 V mini-battery and programmed to operate daily between 4:30 PM and 8:30 AM on the successive day. The passive infrared (PIR) sensor sensitivity was set to the highest level (“high”) to detect

subtle movements. Upon activation, each camera recorded a 20-s video (1920 × 1080, 30 fps), with a 10s trigger interval between consecutive recordings. Camera traps were inspected weekly to replace SD cards and batteries, exclusively between 12:00 PM and 2:00 PM, when cranes were consistently absent from the roost and foraging in nearby fields (Monti et al. 2024). No cranes were ever observed at the roost during inspections. Camera also recorded ambient audio via internal microphones.

2.3 | Video Data Processing and Behavioral Classification

All videos were downloaded and reviewed by an expert observer (FM). Recordings were grouped into “Night units” (4:30 PM–8:30 AM), and each video was assigned accordingly based on its timestamp. Astronomical variables (sunrise, sunset, and twilight phases) were computed using the *suncalc* R package (Agafonkin and Thieurmél 2018), calculated according to the coordinates of the study area and timestamp of each video. Based on these, each video was classified into one of three temporal categories: (1) “Evening” from 4:30 PM (camera activation) until the end of dusk twilight; (2) “Night” from the end of dusk twilight until the beginning of dawn twilight in the morning; and (3) “Morning” from the onset of dawn twilight until 8:30 AM (camera disactivation). Lunar illumination for each date and time was quantified using the “*getIllumination*” function of the R package *suncalc*, which computes the fraction of the moon’s visible surface illuminated by the sun, ranging from 0 (totally dark with no moonlight) to 1 (full moon), following the approach described in Agafonkin and Thieurmél (2018) and further documented by Śmielak (2023). Cloud cover data (continuous values in the range 0–1, from clear to fully covered sky) were retrieved from the ERA5 hourly dataset provided by the Copernicus Climate Change Service (Climate Data Store; Hersbach et al. 2023) for the roost coordinates and study period. As video timestamps had minute- and second-level resolution, each event was assigned a cloud cover value by matching it to the nearest hourly estimate within a ± 30-min window.

Behavioral data were extracted at the individual level. Because cameras did not capture the entire roost simultaneously, flock size was not considered. For each video, all visible individuals were counted. As cranes were unmarked, double counts of individuals entering and leaving the frame could not be fully excluded, as in previous studies through field observations (Beauchamp and McNeil 2003).

Behaviors were classified as: (i) “resting”: if an individual remained inactive throughout the video. The resting posture was characterized by the head tucked under wing, sometimes standing on one leg (Ellis et al. 1998); (ii) “active”: if an individual moved at least once during the video. Within this category, any movement was considered (e.g., walking, preening, flying, vigilance, display behavior, emitting calls, or similar activities different from “resting”). Within the “active” category, two subcategories were identified: (iii) “vigilance” behavior, when an individual displayed an extended neck posture, following the definition used in Monti et al. (2024), and (iv) “display” behavior, with an individual performing typical courtship or social displays, including short flights, jumps, or dance-like

movements (e.g., Dinets 2013). From these data, the following indices were calculated per video: (a) activity ratio, defined as the number of active individuals over the total number of visible individuals counted during the video, used as a proxy for overall activity; (b) vigilance ratio, defined as the number of vigilant individuals over the number of active individuals, used as a proxy for overall alertness. For each video, we also included binary variables indicating the presence (1) or absence (0) of display behavior, with the former defined as the occurrence of at least one display event recorded during the video.

2.4 | Audio Data Processing

Each video recording included an audio track captured by the camera trap’s internal microphone. Because crane vocalizations were often recorded even when individuals were not visible (e.g., recordings triggered by other species or environmental factors), all videos were included in the acoustic analysis. A total of 4095 videos were processed and converted into audio files using a custom R script in combination with the program FFmpeg (v. 8.0 “Huffman”; ffmpeg.org), which converted the original MP4 files into AVI format. The resulting audio files were analyzed using the AI-assisted acoustic recognition software BirdNET Analyzer (v2.1.1; Kahl et al. 2021). A training set ($n = 105$) was initially used to improve classification accuracy and detection of crane calls, including both positive examples (crane calls) and negative examples (“false”), consisting of recordings without vocalizations (ambient noise and non-target species). Acoustic data were then automatically processed in BirdNET Analyzer using the default settings: 3-s segments, minimum confidence threshold = 0.5, 0-s overlap, and detection sensitivity = 1.0. Detections with raw confidence ≥ 0.5 were retained. As the software divides each audio file into multiple segments and filters them according to the confidence threshold, the number of detections did not correspond directly to the number of original videos. This procedure resulted in a total of 26,553 acoustic detections that were classified as presence (1) or absence (0) of crane vocalizations. The output files generated by BirdNET (in .csv format) were subsequently merged into a single dataset in R. To complement these data, temporal and environmental variables (night unit, phase of the night, moon illumination, and cloud cover) were assigned as described above.

3 | Statistical Analyses

Statistical analyses were performed in R (v. 4.3.1; R Core Team 2022). Video and audio datasets were analyzed separately using generalized linear mixed models (GLMMs; Zuur and Ieno 2016). For video data, we fitted four models to assess whether environmental factors influenced crane behavior. Three response variables were modeled: (i) the activity ratio and (ii) the vigilance ratio, both expressed as continuous proportions and modeled with a beta family distribution and logit link (ordered beta parametrization; Kubiñec 2022); and (iii) the presence/absence of display behavior (binary variable: 0 = absent, 1 = present) analyzed with a binomial family distribution and logit link.

Across all video-based models, we included the following predictors: (a) “Phase of the night” (categorical: “Evening,” “Night,”

or “Morning,” reference category: “Night”). (b) “Moon illumination” (continuous: % lunar surface illuminated) and (c) “Cloud cover” (continuous: % sky surface covered by clouds) and their interaction. We also included (d) “Night unit” (integer: ranging from 1 to 49), representing the temporal progression through the wintering season from mid-December to mid-March. Only in the model of the presence or absence of display behavior did we include an additional predictor, namely, (e) “the number of active individuals.” Contrary to models on activity and vigilance, where response variables were expressed as ratios and thus were already standardized by the number of individuals, this variable was included as it may influence the occurrence of social interactions (e.g., displays). In all models, “Night unit” was also included as a random effect to account for repeated observations during the same night.

For audio data, crane vocalization presence (binary: 0 = absent, 1 = present) was modeled with a binomial distribution and a logit link, using the same predictors and random effect, excluding the number of active individuals, as audio files were not necessarily associated with the presence of cranes within the video. The “Night unit” spanned the full audio dataset, covering December 15 to March 13 (range: 1–83). To account for seasonal departure of cranes (Giovacchini 2019), this model was run on both the full dataset and a restricted period (December 15–February 20).

To test whether results were robust to light conditions, all models (both video and audio) were repeated on a subset of data including only the “Night” phase, thus excluding the “Evening” and “Morning” phases (see [Supplementary Materials](#)).

In all global models, neither collinearity between numeric predictors ($r < |0.5|$ in all cases) nor multicollinearity among predictors was found (VIFs < 2). All numeric predictors were scaled to increase model convergence and interpretability of the interactive term. For all global models, all the possible combinations of predictors, including the null model, were evaluated (Harrison et al. 2018). However, the predictor ‘number of active individuals’ in the third model (display behavior) was always retained in all candidate models, as it was needed to standardize the response variable. The model selection used Akaike’s Information Criterion corrected for small sample sizes (AICc). Models were selected if they had $\Delta\text{AICc} \leq 2$, and, among them, all models whose AICc was higher than that of a simpler nested alternative were excluded to avoid retaining overly complex models (Harrison et al. 2018). This procedure resulted in either a single best model or a set of top-ranked models for each response variable. The Akaike model weight was standardized within the subset of selected models. Results of model selections were reported in Tables [SX1–SX10](#). Inference about the effect of any predictor was made using the best model: we estimated coefficients and 95% confidence intervals (CIs) of predictors, assessing whether 95% CIs overlapped “0” to identify informative predictors. For the categorical predictor (Phase of the night), pairwise differences were tested with Tukey post-hoc comparisons, through the *emmeans::glht* function (v. 1.10; Lenth et al. 2018), with the significance level set at 0.05. When individual predictors showed significant main effects but were also involved in a significant interaction, only the interaction term was retained for biological interpretation (Spake et al. 2023). We depicted the marginal effects of informative predictors or

interactions through the package “ggeffects” (Lüdtke 2018), while holding constant, when present, the other numeric predictors at their average values and the phase of the day at the level “Night.” GLMMs and model selections were performed using the functions *glmmTMB::glmmTMB* (Brooks et al. 2017) and *MuMIn::dredge* (Bartón 2020), respectively. Best models were validated through visual inspection of residuals through the “DHARMA” package (Hartig 2022).

4 | Results

A total of 4095 videos were collected during the study period, of which 1394 (34.0%) included cranes. Cranes were observed across 49 night units. Across nights, cranes exhibited consistently high levels of activity (mean: $89.4\% \pm 2.1\%$ active individuals), while vigilance behavior was observed in approximately half of the individuals ($44.8\% \pm 3.9\%$). Display behavior was relatively rare overall with a total of 110 events but showed a clear temporal pattern, being recorded only from late January onwards (starting from January 24, 2023), showing a seasonal increase in social interactions. In all videos, cranes were consistently observed standing in shallow water within the roosting area. All footage was converted to AVI format and analyzed, yielding 26,553 audio records, of which 5328 contained crane vocalizations as detected by BirdNet Analyzer.

4.1 | Temporal and Environmental Drivers of Nocturnal Activity

The proportion of active individuals varied according to different phases of the night (Table 1). Activity levels were the highest in the morning, intermediate in the evening, and the lowest at night (Figure 2A; Table S1). Environmental conditions also influenced activity. Moon illumination had a significant negative effect, with higher illumination associated with lower proportions of active individuals. However, this relationship was strongly modulated by cloud cover, as indicated by the significant interactive effect between moon illumination and cloud cover in the best model (Table 1). Under clear sky conditions, the proportion of active cranes declined sharply with increasing moon illumination, whereas this effect was substantially buffered under overcast conditions (Table 1; Figure 2B). When restricting analyses to the “Night” phase only, a positive effect of the night unit on activity ratio emerged (Table S2; Figure S1A), with nocturnal activity that tended to increase gradually over the wintering period (seasonal progression effect). Additionally, the interaction between moon illumination and cloud cover became even more pronounced (Table S2; Figure S1B), strengthening the evidence from the previous model and indicating that the effect of lunar illumination is strongest under fall darkness conditions and diminishes under overcast conditions (Table S2; Figure S1B).

4.2 | Context-Dependent Variation in Vigilance Across the Night and Season

Vigilance behavior varied significantly across the night. The proportion of individuals exhibiting vigilance varied according to the phase of the night (Table 1), with the highest levels

TABLE 1 | Parameters estimated from the top-ranked GLMM predicting the Activity ratio, Vigilance ratio, Display behavior, and Vocalization, in relation to phase of the night, night unit, moon illumination and cloud cover: Variance of random intercepts (σ^2), predictors' coefficient estimates (β), and their 95% confidence intervals (CIs). The number of data points, that is, sample size, is also indicated (n). An asterisk marks coefficients whose CIs do not include "0". Significant codes were: 0 '****' 0.001 '***' 0.01 '**' 0.05 '.' 0.1 '.' 1.

Response variable	Predictor	β coefficient	95% CI
Activity ratio σ^2 Night unit = 1.999 $n = 1394$	Intercept	1.426	0.761; 2.090 ***
	Phase of the night: Morning	1.031	0.753; 1.308 ***
	Phase of the night: Night	-0.726	-0.884; -0.568 ***
	Night unit	0.425	-0.015; 0.865
	Moon illumination	-0.718	-1.226; -0.209**
	Cloud cover	-0.131	-0.258; -0.004*
	Moon illumination $\times$ Cloud cover	0.197	0.045; 0.348*
Vigilance ratio σ^2 Night unit = 0.079 $n = 1296$	Intercept	-0.126	-0.298; 0.046
	Phase of the night: Morning	0.509	0.353; 0.666***
	Phase of the night: Night	0.221	0.086; 0.357**
	Night unit	0.262	0.145; 0.378***
	Moon illumination	-0.156	-0.301; -0.010*
	Cloud cover	0.057	-0.024; 0.138
	Moon illumination $\times$ Cloud cover	0.075	-0.005; 0.157
Display behavior σ^2 Night unit < 0.001 $n = 1394$	Intercept	-4.567	-5.384; -3.750***
	Phase of the night: Morning	1.201	0.307; 2.094**
	Phase of the night: Night	2.091	1.277; 2.904***
	N active individuals	0.502	0.282; 0.723 ***
	Night unit	1.350	0.823; 1.876***
	Moon illumination	0.374	0.113; 0.635**
	Cloud cover	-0.362	-0.427; -0.296 ***
Vocalization σ^2 Night unit = 4.912 $n = 26553$	Phase of the night: Evening	-5.422	-6.029; -4.815***
	Phase of the night: Night	-1.328	-1.430; -1.225***
	Moon illumination $\times$ Cloud cover	0.175	0.114; 0.236***
	Intercept	-1.550	-2.096; -1.005***
	Moon illumination	-1.670	-2.205; -1.134***
	Cloud cover	-0.362	-0.427; -0.296 ***
	Phase of the night: Evening	-5.422	-6.029; -4.815***
Vocalization_subset σ^2 Night unit = 4.751 $n = 19349$	Phase of the night: Night	-1.328	-1.430; -1.225***
	Moon illumination $\times$ Cloud cover	0.175	0.114; 0.236***
	Intercept	-0.666	-1.277; -0.055*
	Moon illumination	-1.594	-2.277; -0.911 ***
	Night unit	0.376	-0.068; 0.822
	Cloud cover	-0.322	-0.404; -0.239***
	Phase of the night: Evening	-6.490	-7.481; -5.500***
	Phase of the night: Night	-1.389	-1.500; -1.278***
	Moon illumination $\times$ Cloud cover	0.115	0.039; 0.191**

in the morning, intermediate at night, and the lowest in the evening, when cranes return to their nocturnal roost at the end of diurnal activities (Table S1; Figure 3A). Thus, heightened alertness occurred prior to departure from the roost, indicatively between 6:30 and 8:00 AM. In addition, a clear seasonal trend was observed. The proportion of individuals exhibiting vigilance

increased over time as winter progressed (Table 1; Figure 3B). Vigilance decreased under brighter moon illumination (Table 1; Figure 3C), and the interaction between moon illumination and cloud cover was not retained (Table 1). When running the alternative model on the "Night" phase only, the positive effect of the seasonal progression was confirmed (Table S2; Figure S2A).

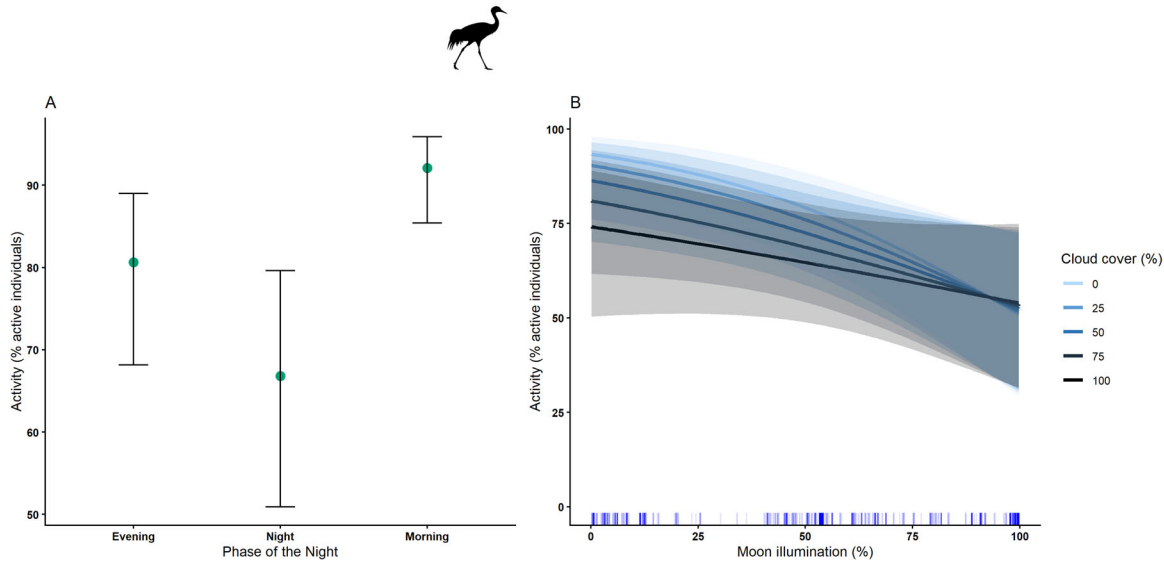


FIGURE 2 | Predicted effects of informative predictors on activity. (A) The effect of the phase of the night cycle (see Table S1, for post-hoc pairwise tests). (B) The interactive effect between moon illumination and cloud cover. Predicted values and 95% confidence intervals are depicted (respectively filled dots and error bar, for categorical predictor and lines and bands, for numeric predictors). For the effects of numeric predictors, the marks along the x-axis show the distribution of observed values.

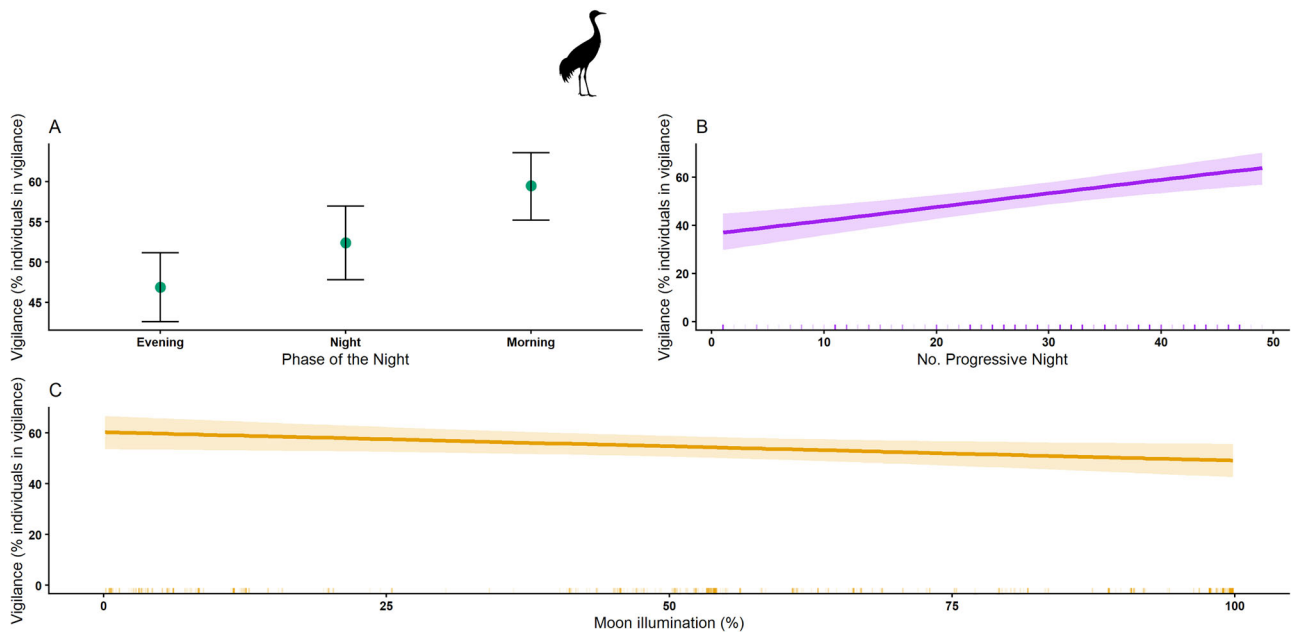


FIGURE 3 | Predicted effects of informative predictors on the percentage of individuals in vigilance. (A) The effect of the phase of the night cycle (see Table S1, for post-hoc pairwise tests). (B) The positive effect of the date (No. of progressive night during the year). (C) The negative effect of moon illumination. Predicted values and 95% confidence intervals are depicted (respectively filled dots and error bar, for categorical predictor and lines and bands, for numeric predictors). For the effects of numeric predictors, the marks along the x-axis show the distribution of observed values.

However, the effect of moon illumination became conditional on cloud cover. Vigilance decreased with increasing moon illumination when the sky was not covered by clouds, yet this relationship weakened and even reversed under overcast conditions; that is, vigilance increased with increasing moon illumination when the sky was overcast (Table S2; Figure S2B). No predator was detected in any of the video recordings during the study period, precluding analyses of direct predator-related effects on alert behaviors.

4.3 | Seasonal and Environmental Modulation of Social Display Behavior

Display behavior showed distinct temporal, seasonal, and environmental patterns. The probability of exhibiting a display behavior was the highest during the night, intermediate in the morning, and the lowest in the evening (Table S1; Figure 4A), with social interactions predominantly occurring after roost establishment. The occurrence of display behavior increased with the proportion

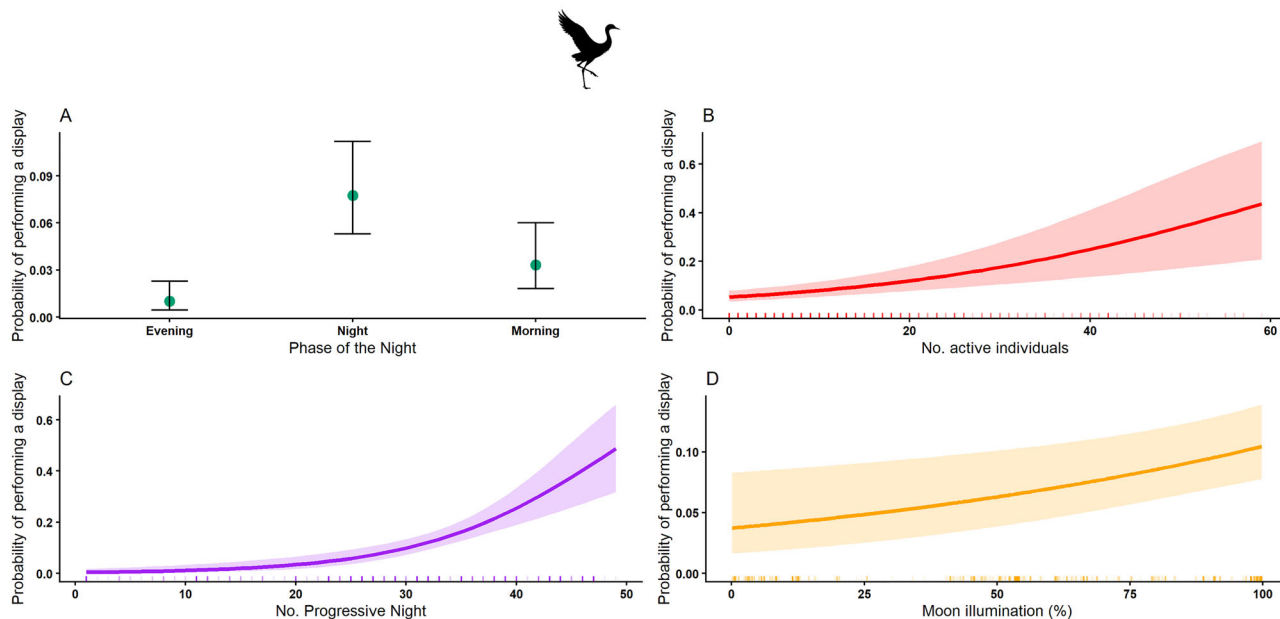


FIGURE 4 | Predicted effects of informative predictors on the probability of performing a display. (A) The effect of the phase of the night cycle (see Table S1, for post-hoc pairwise tests). (B) The positive effect of the number of active individuals. (C) The positive effect of the date (No. of progressive night during the year). (D) The positive effect of moon illumination. Predicted values and 95% confidence intervals are depicted (respectively filled dots and error bar, for categorical predictor and lines and bands, for numeric predictors). For the effects of numeric predictors, the marks along the x-axis show the distribution of observed values.

of active individuals (Table 1; Figure 4B). There was also a significant seasonal effect (night unit), with displays becoming more frequent over time as winter progressed (Figure 4C) and steadily increasing from the second half of January onwards. Furthermore, the probability of showing display behavior increased with increasing moon illumination, contrary to the patterns observed for both activity and vigilance (Figure 4D). When running the alternative model on the “Night” phase only, the positive seasonal effect was confirmed (Table S2; Figure S3A), as was the positive effect of the number of active individuals on the occurrence of display behavior (Table S2; Figure S3B). In contrast, the effect of moon illumination was not retained in the night-only analysis (Table S2).

4.4 | Effects of Seasonal and Nocturnal Light Conditions on Vocal Activity

Vocal activity varied across the night. The probability of performing a call was the highest in the morning, intermediate at night, and the lowest in the evening (Table S1; Figure 5A), mirroring the temporal patterns observed for activity and vigilance. Cranes generally reduced their vocal activity with increasing moon illumination, although this effect was moderated by cloud cover: the negative effect of moon illumination was strongest under clear skies and weakened under overcast conditions (Table 1; Figure 5B). Seasonal effects were not retained, and the effect of the night unit was not supported in the original model. This interpretation was supported by the restricted analysis on a subset of data (until 20 February), where results were fully consistent with the original model (Table 1). When running the alternative model on the full dataset but for the “Night” phase only, vocal activity showed a negative relationship with night units (Table S2;

Figure S4A). In this model, the interactive effect between moon illumination and cloud cover was confirmed as for the original model (Table S2; Figure S4B). When repeating this last model (“Night” phase only) applied on the subset of data (until 20 February), the effect of the night unit was no longer retained, whereas both moon illumination and cloud cover exerted a significant negative effect on vocal activity (Table S2; Figure S5A and Figure S5B, respectively).

5 | Discussion

By integrating behavioral, ecological, and environmental dimensions, we provide a comprehensive view of the mechanisms and drivers of nocturnal behavior in a diurnal, gregarious bird. Our study shows that Common cranes adjust nocturnal activity, vigilance, display, and vocal behaviors in response to varying environmental conditions, revealing flexible behavioral tactics that balance antipredatory demands while navigating nighttime risks.

As per our first working hypothesis, activity patterns were consistent with the species’ diurnal rhythm: cranes were generally most active in the morning, gradually decreasing activity toward nighttime. During the morning, cranes engaged in frequent vigilance and vocalizations, behaviors that likely served to acquire social information from conspecifics before leaving the nocturnal roost and deciding to depart for daily foraging activities (e.g., Beauchamp 2010, 2015). Such vigilance-based social information gathering reflects a mechanism also observed in other gregarious species (Beauchamp 2015). Notably, cranes consistently departed from nocturnal roost almost exclusively before 8:00 AM, with only one record (0.07% of the total) of later departures, high-

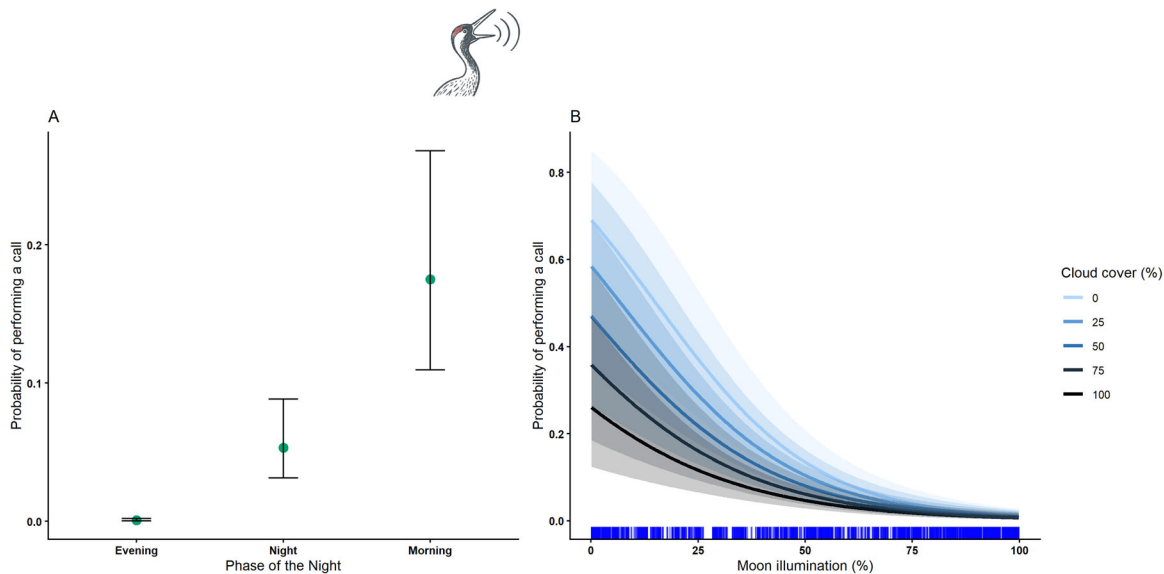


FIGURE 5 | Predicted effects of informative predictors on the probability of performing a call. (A) The effect of the phase of the night cycle (see Table S1, for post-hoc pairwise tests). (B) The interactive effect between moon illumination and cloud cover. Predicted values and 95% confidence intervals are depicted (respectively filled dots and error bar, for categorical predictor and lines and bands, for numeric predictors). For the effects of numeric predictors, the marks along the x-axis show the distribution of observed values.

lighting strong temporal consistency in daily activity. Conversely, evenings were characterized by declining activity as individuals returned to the roost, with nighttime marking the primary resting phase, as initially supposed because of the minimal daytime rest recorded in the same area and population (Monti et al. 2024).

However, despite being primarily diurnal, cranes exhibited a higher-than-expected level of nocturnal activity, which varied with environmental conditions. Activity was reduced during bright, clear nights. This pattern contrasts with studies conducted in semi-controlled conditions, reporting that nocturnal illumination, especially artificial light, can disrupt sleep or resting cycles (van Hasselt et al. 2020a, 2020b). In our study, conducted under natural conditions, we suggest that this reduction in activity during well-lit nights may indicate that brief awakenings suffice for visual monitoring of conspecifics and surroundings, thereby minimizing prolonged vigilance (Beauchamp 2015). This pattern is similar to the daytime vigilance behavior observed in cranes, which adopt repeated but short head-up postures (Monti et al. 2024). An alternative explanation is that the apparent lunar-phobic response of cranes may reflect an adaptive strategy to reduce exposure to predators whose activity or hunting efficiency increases under brighter moonlight (e.g., Lazzeri et al. 2024). Nevertheless, any role of predation risk should be inferred cautiously, as no predator was detected during the study period, although perceived predation risk may persist even in the absence of observed predators. Conversely, during darker nights, we recorded an increased nocturnal activity and vigilance, a pattern suggestive of heightened alertness under low-visibility conditions, although this interpretation remains indirect given the lack of direct measures of sleep or resting states. In addition to that, moon illumination and cloud cover interacted, modulating perceived safety and visual capability (Śmielak 2023). Cloud cover dampened the strong effect of a full moon, whereas during new moon nights the influence of clouds was negligible, likely because

of the already minimal ambient light. These findings emphasize how Common cranes flexibly adjust nocturnal behaviors in response to environmental cues, balancing rest with the need to remain alert under variable nighttime conditions.

Display behaviors exhibited distinct patterns compared to activity and vigilance. Displays involve highly stereotyped and synchronous movements, including dances and flight-jump displays, typically associated with the pre-breeding period and used to reinforce social and pair bonds (Ellis et al. 1998; Dinets 2013). We found that these behaviors were more frequent under well-lit conditions, even during the central hours of the night (Video S1), suggesting that cranes might use moonlight to communicate and enhance visual signaling with conspecifics. A similar role of moonlight has been documented in another diurnal bird species, the African houbara bustard (*Chlamydotis undulata*), in which moonlight was shown to trigger nocturnal display activity during the breeding season (Alonso et al. 2021). In this context, increased visibility may facilitate social signaling and the performance of visually mediated behaviors (Kурvers and Hoelker 2015; Pentecari et al. 2011). Moreover, display behavior was more likely to occur in the presence of larger numbers of active individuals, probably due to stronger social facilitation, which promotes these stereotyped behaviors when several conspecifics are present (Tobias et al. 2016; Sánchez and Mennill 2024).

With regard to the migratory species' ecology, both vigilance and display behaviors increased as winter progressed, reflecting interactions between environmental cues, nocturnal illumination, and the annual migratory cycle. These findings align with known processes in migratory species, where preparatory physiological changes, such as migratory restlessness, modulate nocturnal behaviors (Berthold 2001; Newton 2010). Comparable patterns have been reported in other migratory species. For instance, in the Red-headed bunting (*Emberiza bruniceps*), migratory restlessness coincides with increased nocturnal activity (Yadav et al. 2021).

We also stress that display behaviors were firstly detected in the second half of January (24/01) and intensified thereafter, suggesting that nocturnal illumination and the progression of the annual cycle may interactively influence social behavioral expression. At the same time, this seasonal increase may also reflect changes in social interactions and pair-bond reinforcement prior to spring migration. These mechanisms are not mutually exclusive and may jointly contribute to the observed patterns.

Finally, vocal activity, which plays a key role in social communication (Seppänen et al. 2007), showed the opposite trend to displays, being less frequent under bright moonlight. This pattern may reflect an adaptive strategy to minimize the risk of attracting predators (e.g., Budka and Kokociński 2021) when individuals are more visible in well-lit conditions, as documented in other bird species (e.g., Mougeot and Bretagnolle 2000a). Conversely, during darker or overcast nights, vocalizations increased, likely to maintain acoustic contact among different flocks within the roost or to facilitate the aggregation of isolated individuals into groups. In open landscapes, such as the wintering grounds typically used by Common cranes, sound can travel efficiently. However, vocalizations may also reveal the position of individuals to nocturnal predators, thereby increasing predation risk. Therefore, the observed reduction in calling during bright nights likely represents a form of risk-sensitive communication, balancing the need to maintain group contact with the need to minimize detectability. Moreover, temporal analyses indicated that the effect of night units (i.e., seasonal progression) on vocal activity was relatively weak (or absent when focusing on the subset until 20 February), suggesting that broader phenological factors may overshadow short-term changes in nocturnal calling.

In synthesis, our results underscore the complex interplay between environmental conditions, social context, and temporal factors in shaping nocturnal behaviors of a diurnal species. The observed patterns suggest that Common cranes adjust multiple behavioral dimensions adaptively, balancing antipredatory needs, social facilitation, and ecological constraints. Extending similar studies across additional sites throughout the species' range, encompassing varying levels of anthropogenic disturbance or artificial lighting, would allow assessment of whether the observed nocturnal strategies represent a general pattern or a context-dependent response to local conditions. Comparisons between near-natural baseline settings, such as our study site, and areas increasingly affected by human disturbance or artificial illumination could indeed further clarify how anthropogenic pressures influence nocturnal behavior and social dynamics in cranes (e.g., Wang et al. 2011; Luo et al. 2023). Ultimately, such studies would contribute to a broader understanding of how environmental and human-related factors interact to shape behavioral flexibility in diurnal birds.

6 | Conclusions

Common cranes exhibited remarkable behavioral flexibility at night, adjusting activity, vigilance, display, and vocal behaviors in response to environmental cues. Bright, clear conditions suppressed activity and calling, likely to reduce predation risk, whereas darker or cloudier nights enhanced them, probably for maintaining social cohesion. Display behaviors, by contrast,

increased under illuminated conditions, suggesting adaptive use of moon illumination to facilitate visual communication and signaling. Overall, these findings suggest that diurnal, social birds can finely balance safety, communication, and social interactions under variable nighttime conditions. Environmental factors such as lunar illumination and cloud cover are key drivers of nocturnal behavioral modulation, highlighting the ecological and evolutionary significance of external cues in shaping adaptive responses in diurnal species. More broadly, our results show that species traditionally considered diurnal may flexibly exploit the nocturnal environment and adjust different behavioral components according to prevailing environmental conditions. This capacity may be more widespread than previously recognized (e.g., Alonso et al. 2021) and underscores the importance of accounting for 24-h and seasonal changes in animal behavior. Future work would be necessary to identify the adaptive significance of such behavioral modulation, thereby improving our understanding of how external *stimuli* may act as a selective force shaping nocturnal behavioral strategies.

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Ethics Statement

The protocol for the research project was approved by the Scientific Committee of the Maremma Regional Park Agency within which the work was undertaken and that it conforms to the provisions of the Declaration of Helsinki (as revised in Edinburgh 2000), available at <http://www.wma.net/e/policy/b3.htm>.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting the findings of this study are provided as [Supplementary Material](#).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supporting File 1: inz270195-sup-0001-SuppMat.docx **Table S1**

Results of significant post-hoc tests conducted with Tukey's method for multiple comparisons on the models fitted on the full dataset. **Table S2** Parameters estimated from the top-ranked GLMM predicting the Activity ratio (first model selection), Vigilance ratio (second model selection), Display behavior (third model selection) and Vocalization (fourth model selection) on a subset of data referring to the "Night" phase only and in relation to date, moon illumination and cloud cover: variance of random intercepts (σ^2), predictors' coefficient estimates (β), and their 95% confidence intervals (CIs). **Figure S1** Predicted effects on activity during the "Night" phase only. (A) Effect of the date (No. of progressive night during the year). **Figure S2** Predicted effects on vigilance during the "Night" phase only. **Figure S3** Predicted effects on display behavior during the "Night" phase only. **Figure S4** Predicted effects on the probability of performing a call during the "Night" phase only. **Figure S5** Predicted effects on the probability of performing a call on a temporal subset spanning December 15, 2022, to February 20, 2023, and during the "Night" phase only. **Video S1** Video from a camera trap showing the display behavior of several common cranes on the night of February 2, 2023, at 12:08 AM. **Supporting File 2:** Video S1.